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THE CONDOR

VOLUME 58 SEPTEMBER-OCTOBER, 1956 NUMBER 5

OBSERVATIONS ON A SOOTY GROUSE POPULATION AT SAGE HEN CREEK, CALIFORNIA

By ROBERT S. HOFFMANN

In recent years there has been considerable interest in two separate aspects of the biology of Blue Grouse (*Dendragapus*). The first of these is the controversy concerning their taxonomy. The genus is widely distributed in the coniferous forests of the western states and consists of two groups of races recognized by some as separate species: the *fuliginosus* group, or Sooty Grouse, along the Pacific coast, and the *obscurus* group, or Dusky Grouse, in the Great Basin and Rocky Mountain areas. Originally these two groups were placed under the name *Dendragapus obscurus* on the basis of supposed intergradation (Bendire, 1892:41, 44, 50). The work of Brooks (1912, 1926, 1929) and Swarth (1922, 1926), however, led to their separation in the fourth edition of the A.O.U. Check-list (1931) into coastal and interior species. This split stood until the publication of the 19th Supplement to the A.O.U. Check-list (1944) when, following Peters (1934), *D. fuliginosus* and its subspecies were replaced under *D. obscurus*. Although at that time some doubt was still expressed about the correctness of this merger (Grinnell and Miller, 1944:113), intergradation in northern Washington and southern British Columbia between the races *fuliginosus* and *pallidus* has now been reported by several authors (Munro and Cowan, 1947:89; Carl, Guiguet, and Hardy, 1952:86; Jewett, Taylor, Shaw, and Aldrich, 1953:200).

The taxonomy of these grouse must rest upon the fact of intergradation between the two groups of races. Regardless of the final taxonomic disposition of the Blue Grouse, there are certain biological contrasts between the *fuliginosus* and *obscurus* groups which remain worthy of emphasis, even if they are not considered to justify specific separation of the racial groups.

The second aspect of Blue Grouse biology to arouse recent interest relates to the nature of population fluctuations exhibited by these birds. Until fairly recently it has been widely assumed that their populations also undergo the regular, almost periodic, fluctuations in density that have been described for other species of grouse—the "grouse cycle" or "ten-year cycle." Lately, the assumption that Blue Grouse are cyclic has been questioned (Bendell, 1955*a*), and the matter has not been settled to date.

A study of the coastal form, or Sooty Grouse (*D. fuliginosus*), in the vicinity of Sage Hen Creek, Nevada County, California, from December, 1951, until June, 1955, provided observations on a small, relatively isolated population. Comparison of the behavior and density fluctuations in this population with previous descriptions of other populations is pertinent to the current problems of taxonomy and population fluctuations in the genus *Dendragapus*.

BEHAVIOR OF THE SAGE HEN CREEK POPULATION

The local study area (fig. 1) consists of the basin enclosing three headwater tributaries of Sage Hen Creek, at an altitude of about 7000 feet. The area, of about one-half square mile, is partly isolated from the surrounding ridges by dense brush fields of

Ceanothus and *Arctostaphylos*. White firs (*Abies concolor*) are the predominant trees, with a few red firs (*Abies magnifica*), Jeffrey pines (*Pinus jeffreyi*) and western white pines (*Pinus monticola*). A dense riparian growth of willows (*Salix* sp.) and alders (*Alnus tenuifolia*) occurs along the streamside, and aspens (*Populus tremuloides*) and lodgepole pines (*Pinus contorta*) are present on moist soil sites.

Migration.—Various authors (Anthony, 1903; Grinnell, Bryant, and Storer, 1918; Marshall, 1946; Wing, 1947; Bendell, 1955*b*) agree that Blue Grouse usually perform an altitudinal migration from their winter habitat in the coniferous forests on the high

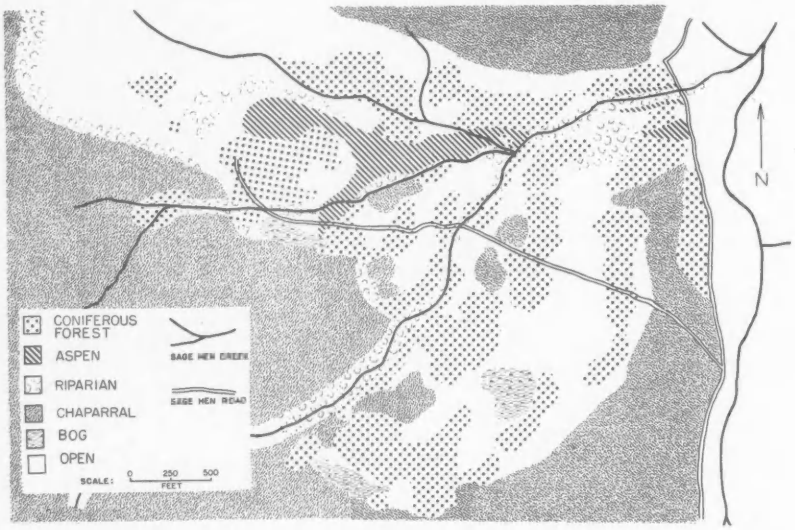


Fig. 1. Map of study area showing vegetation types around headwaters of Sage Hen Creek, Nevada County, California; map prepared from United States Forest Service aerial photograph (C.D.J. 12–56, 6–27–39) and ground survey.

ridges down to their breeding range in lower, often more open country. This movement occurs in early spring (March or April), prior to any breeding activity, and is accomplished in a relatively short period of time. After breeding, males begin to move back upslope in July, and the hens and chicks follow in August and September. Normally, then, breeding and winter ranges are completely separated.

This was not true of the population at Sage Hen Creek. Although only observational evidence is available, it is fairly certain that the Sooty Grouse wintering on the study area were the same ones which bred there. No extensive altitudinal migration took place, and although movements of 500 to 600 yards probably occurred, from a winter roost site on a ridge down to a nesting site in the aspens near the creek, these distances are within the magnitude of the normal daily range of the grouse. Other populations of Blue Grouse have been reported to reside in one area throughout the year, either at high altitudes (Swarth, 1926:83; Johnson, 1929:292–293; Schottelius, MS; Jewett *et al.*, 1953:197) or low (Jewett *et al., loc. cit.*).

Flocking.—A second aspect of the behavior of the local population which is at variance with the reported behavior of other Blue Grouse concerns flock formation. The

normal social organization in both *fuliginosus* and *obscurus* groups is that of a small flock throughout most of the year. Following the decline of courtship behavior, adult males associate in bands of five to six birds during their uphill migration to the winter range (Fowle, MS; Wing, Beer, and Tidyman, 1944:439; Caswell, MS). Similarly, a shuffling and combining of hens and their broods into loose flocks occurs later in the summer, prior to the uphill migration (Wing, Beer, and Tidyman, *op. cit.*:435 ff.; Bendell, 1955*b*:377). On the winter range of *D. obscurus pallidus,* Caswell (MS) reports flocks of six to ten grouse, including adult males, as frequent. Bendire (1889:33), Munro (1919:66), and Beer (1943:34) have also remarked on winter groups.

No flocks of grouse, excluding hens with broods, were noted in the course of the study of the Sage Hen Creek population. In a total of 43 encounters involving 51 grouse, 35 solitary birds and 8 pairs were seen. Of the pairs, four consisted of a male and female, one of two males, and three of unknown sex. While these observations are biased by the fact that most of the field work was done in the spring and early summer when solitary behavior is normal, I feel that the data indicate a real behavioral difference in this population.

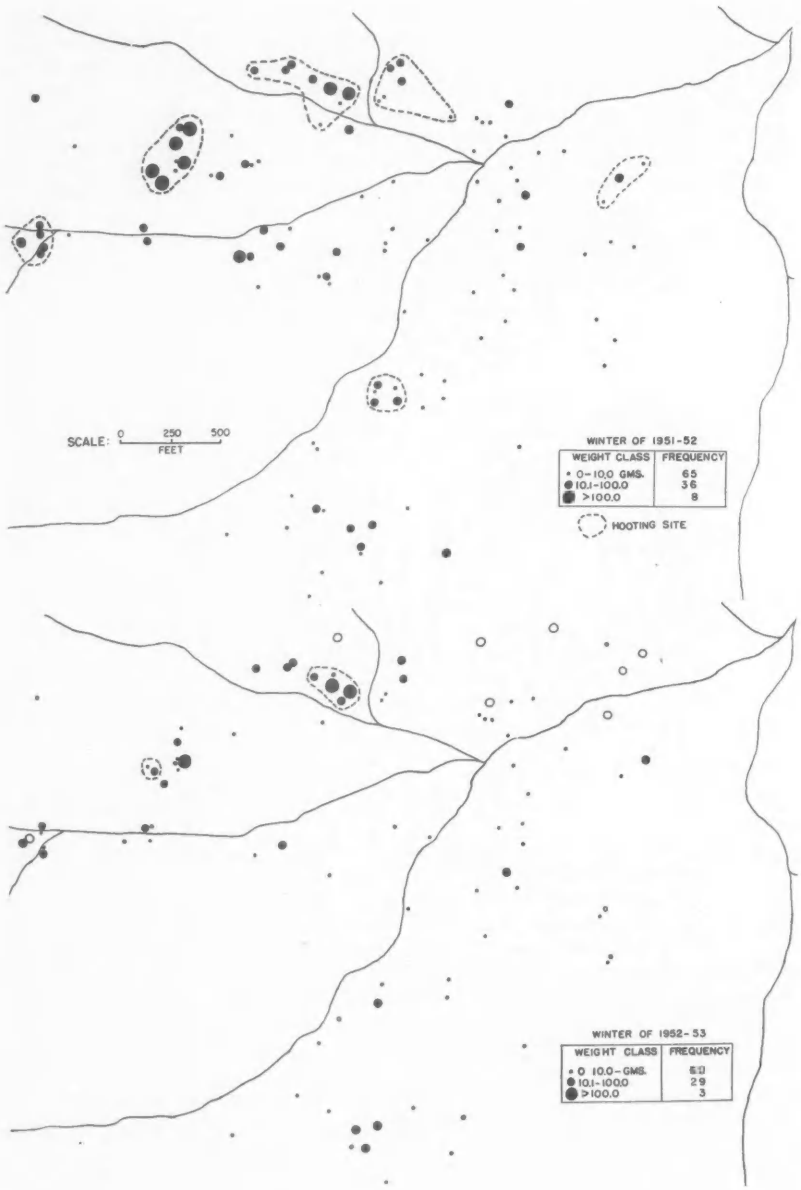
Breeding behavior.—Observations on behavior of the Sooty Grouse in the spring breeding period were made in the course of obtaining a tally of displaying male birds. The count of these hooting males consisted merely of following the sound produced by a displaying cock until he was located and then noting his position on a map. In some instances the bird could not actually be seen, in which event approximate locations were noted. The whole study area was covered for a series of ten days in 1952, seven days in 1953, five days in 1954, and five days in 1955.

Figure 2 shows the occurrence of hooting male grouse in the springs of 1952, 1953, and 1954. Each "hooter" was apparently restricted to a small area, in which he could be found displaying almost every day throughout the courtship period. From these observations it is inferred that adult male grouse in this population are territorial during the courtship period, as were the Sooty Grouse cocks described by Bendell (1955*b*:369).

The volume, frequency, and cadence of hoots of displaying cocks at Sage Hen Creek is the same as that described by earlier workers for the *fuliginosus* group (Bent, 1932: 105; Grinnell, Bryant, and Storer, 1918:548; Edson, 1925:227). Usually a hooting bird was situated near the top of a white fir, but occasionally he might be found hooting from a Jeffrey or lodgepole pine. Two separate birds were observed hooting from the ground on May 17, 1953.

In 1952, the first hooting was heard on the study area on May 10. In the month prior to this date, full days were spent on the area on April 11, 19, 20, and May 1, 4, 9. Negative observations on these dates indicate that active hooting began in the second week of May. Hooting seems to have begun earlier in the springs of 1951, 1953, and 1954. A. S. Leopold (unpublished field notes) found hooting in full swing after the middle of April in 1951. My field notes record no hooting on April 12, 1953, and active hooting on April 28, 1953, so hooting must have begun after mid-April in that year. In 1954, cock grouse were hooting on April 28, but no observations are available for the period prior to this date. It is concluded that hooting began at least by the last week of April in that year.

The factor that most obviously correlates with the onset of hooting and the courtship period in the male grouse is the persistence of snow cover in the spring. The years 1951, 1953, and 1954 approached the average in this respect, with snow cover on the study area disappearing around the first of May. In contrast, a snow cover was present for a full month longer in 1952, following a winter of record snowfall. This abnormally persistent snow cover may have inhibited the normal onset of courtship behavior in the


SCALE: 0 250 500
FEET
WINTER OF 1951-52
WEIGHT CLASS | FREQUENCY
0-10.0 GMS. | 65
10.1-100.0 | 36
>100.0 | 8
HOOTING SITE
WINTER OF 1952-53
WEIGHT CLASS | FREQUENCY
0 10.0-GMS. | 50
10.1-100.0 | 29
>100.0 | 3

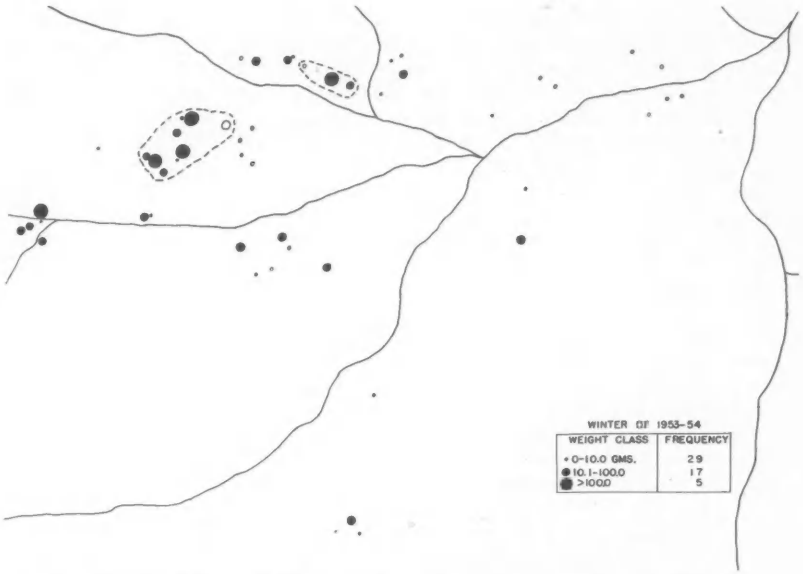


Fig. 2. Distribution of winter roost sites and hooting territories of breeding male grouse in the following spring, for 1951–52, 1952–53 (see opposite page), and 1953–54. Weight class of roost sites refers to total weight of droppings collected at that site (see text). Open circles in last two years indicate roost sites not occupied in previous winter.

male grouse, perhaps by delaying the normal transition to spring foods from the winter diet of fir needles.

The date of hooting cessation also appeared to be unusual in 1952. No hooting was heard after May 30, although a great deal of time was spent in the field. In contrast, prolonged, regular hooting was heard throughout June of the next two years, and even as late as July 6, 8, and 27, 1953, and July 4 and 5, 1954. No reason for the abrupt termination of hooting in 1952 is apparent.

Winter behavior.—As has been well described by previous authors (Belding, 1892; Grinnell, Bryant, and Storer, 1918; Beer, 1943; Stewart, 1944; Marshall, 1946), Blue Grouse ascend coniferous trees of several kinds with the approach of winter and remain in these trees most of the time, feeding on their needles, until the melting of the snow cover in spring once more allows them to obtain food from the ground. White fir is by far the most favored roost tree in the Sage Hen Creek area. The distribution of winter roost sites in three winters is indicated in figure 2. A comparison of this distribution with the map of the study area in figure 1 shows that the heaviest winter use of the fir tree roosts was concentrated in the area surrounding the only extensive aspen stand. This pattern held for all three winters, in both high and low population densities.

Several explanations for this correlation suggest themselves. One is the presence of permanent springs in the aspen grove that tend to remain free of snow throughout much of the winter, thus providing a source of accessible water and perhaps a few food plants. A second possibility is that the grouse favor the southern exposure of this slope.

It is apparent from figure 2 that some roost sites are utilized to a much greater

degree than are others (Beer, 1943:34; Wing, 1947:506). However, only a small part of the total white fir on the areas was used for roosts. The factors influencing this selection on the part of the grouse are not known. No obvious correlation existed between size or dispersion of the trees and degree of winter use. A further point is that each grouse probably roosts in a number of trees in the course of the winter and does not remain in just one or a few trees. Caswell (MS) also found this to be true in Idaho.

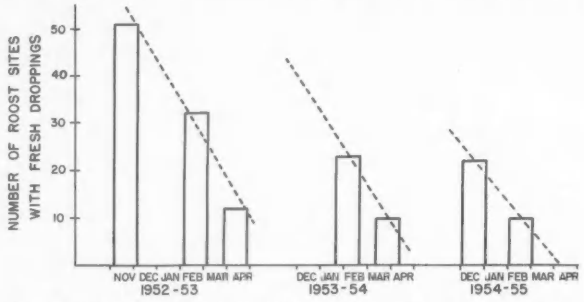


Fig. 3. Trend in numbers of occupied roost sites on the study area during the winters of 1952–53, 1953–54, and 1954–55. A roost site was considered occupied if fresh grouse droppings were visible on the snow surface beneath the roost trees.

Figure 3 indicates that a progressive decline in the number of roost sites in current use occurred in the course of each winter. This decline might be due to progressive winter mortality among the grouse, although there is no evidence to support this conjecture.

Discussion.—The morphological differences between the *fuliginosus* and *obscurus* groups of the genus *Dendragapus* have been thoroughly discussed by earlier authors. These differences include well-developed, orange gular air sacs coupled with a loud hoot during courtship in the coastal Sooty Grouse and less fully developed, purplish gular sacs that produce a soft hoot in the inland Dusky Grouse. Tail shape is also reported to be different in the two groups (Brooks, 1912:252, 1926:282–283; Swarth, 1922:204, 1926:80), as is coloration of the downy chicks (Moffitt, 1938).

Behavioral differences between the two groups of Blue Grouse have not been emphasized to the same extent as morphological differences. Brooks (1926:282–283) mentioned that in his experience the Dusky Grouse (subspecies *richardsoni*) "always utters [its courtship] hooting from the ground," whereas Sooty Grouse hoot from "high up in a coniferous tree." This difference seems to hold in the majority of cases (Wing, 1946: 157), but evidence from the present study and others (Edson, 1925:228; Johnson, 1929:292) shows that the Sooty Grouse, at least, may deviate from its usual behavior and occasionally hoot from the ground.

Another behavioral difference between the two groups for which some evidence is available concerns territoriality in the breeding males. Bendell (1955*b*:369) is the first author to give an adequate description of such territorial behavior, for the subspecies *fuliginosus*. He found that in a population on Vancouver Island the adult males were strongly territorial when hooting. Adult males always returned to the same territory each spring, but if a male failed to return, his place was taken by a new male, or the adjacent male expanded his own territory. Fowle (MS) also came to the conclusion that Sooty Grouse were territorial when hooting, on the basis of general observations in the same area. In contrast to this well-marked territorialism among displaying males of the

juliginosus group, Schottelius (MS) and Caswell (MS) found that no territorialism was apparent in hooting males of the race *Dendragapus obscurus pallidus*. Schottelius reported as many as seven males in simultaneous display on a two-acre "hooting area." However, this conclusion was based on observational evidence alone.

These several behavioral differences may be correlated with the different habitat preferences of the two groups in the breeding season. The North American grouse that indulge in communal courtship display are *Centrocercus, Tympanuchus, Pedicoecetes,* and, as noted above, there may be at least a tendency toward this in the *obscurus* group of *Dendragapus*. Such communal display is performed on the ground in open country. In the *juliginosus* group of *Dendragapus,* and in *Canachites* and *Bonasa,* the courtship display is solitary and is performed in denser cover, usually from a tree or log.

Throughout the summer, the *juliginosus* group, along the humid Pacific coast, in general inhabits fairly dense cover of aspen groves and meadow edges adjacent to dense coniferous forests. The *obscurus* group of the more arid interior, on the other hand, often moves out onto quite open bunch grass and sagebrush-grass areas to breed. Brooks (1926:283) first emphasized this difference. Corroboration of his opinion is found in the comments of many authors (Anthony, 1903:26; Saunders, 1914:130; Lee, 1936: 122; Wing, Beer, and Tidyman, 1944:429; Marshall, 1946:43, 46, 50; Wing, 1947: 508; Schottelius, MS; Jewett, *et al.,* 1953:193–195; Caswell, MS, for the *obscurus* group; and Grinnell, Bryant, and Storer, 1918:547; Dawson, 1923:1591–1595; Burleigh, 1929:509; Bent, 1932:106; Gabrielson and Jewett, 1940:210; Grinnell and Miller, 1944:113–116; and Jewett, *et al.,* 1953:198, for the *juliginosus* group). A possible exception to this generalization is the nesting behavior of the subspecies *obscurus* in Colorado and Wyoming, since Rockwell (1908:161), Neilson (1926:99), Skinner (1927:210, 213), and Bent (1932:91) consider the nesting range to be within the area of aspen and conifer timber.

The population of Sooty Grouse at Sage Hen Creek, although inhabiting the eastern edge of the range of the *juliginosus* group, on the arid, Great Basin side of the Sierra Nevada, seems, in its behavior, to resemble *D. f. juliginosus* from the humid coastal forests rather than any member of the *obscurus* group from the Great Basin. Displaying males were found day after day and year after year at the same hooting sites, and each site was well separated from adjoining sites. From these observations, territorial behavior is inferred. Furthermore, almost all hooting was done from trees.

Previous mention has been made of the atypical, non-migratory habits of the population. A downhill migration along Sage Hen Creek for a distance of about eight miles would bring the population from its present year-round range to an area of sagebrush-bunch grass along the lower part of the creek and the Little Truckee River. This open terrain of sagebrush and bunch grass is similar to the summer range used by some populations of Dusky Grouse, but it is not typical of breeding areas used by Sooty Grouse. Whether or not the grouse population in the Sage Hen basin was ever migratory is not known. It is conceivable that altitudinal migration might have taken place in the past, when, according to the testimony of old residents of the area, the grouse population was denser. The present lack of flocking behavior in the Sage Hen Creek population might also be associated with low population density. On the other hand, the absence of pronounced altitudinal migration could be a behavioral character relatively fixed genetically in this population.

POPULATION FLUCTUATIONS IN BLUE GROUSE

In spite of a voluminous literature on the general topic of grouse "cycles," very little is known concerning population fluctuations in the Blue Grouse. Leopold (1933:58)

and Wing (1947:510) both state that Blue Grouse are cyclic, but they do not cite any specific data. Bendell (1955*a*:221) has recently introduced a proper note of caution by questioning the uncritical assumption that Blue Grouse populations must be cyclic merely because other grouse exhibit this pattern of population change.

Historical evidence for cycles in Blue Grouse.—By following the procedure of two recent investigators (Buckley, 1954; Williams, 1954), an indication of the trends in

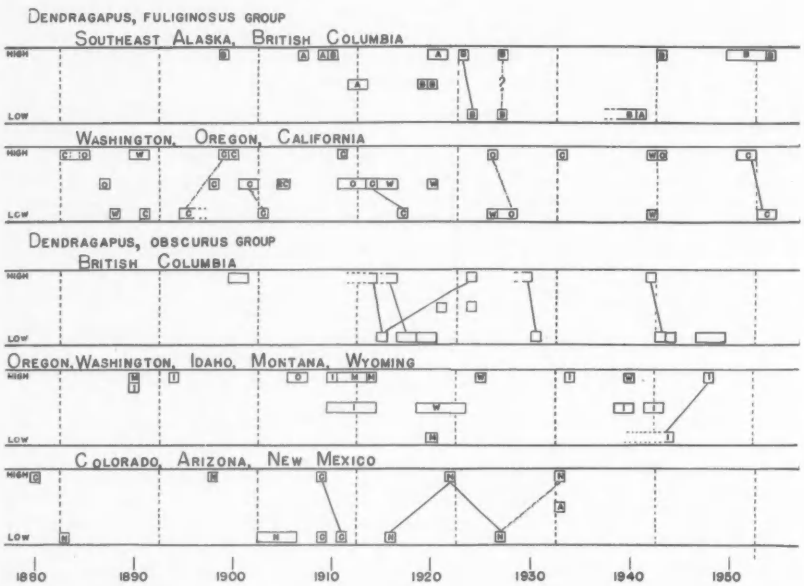


Fig. 4. Relative abundance of Blue Grouse, 1880–1954, plotted according to whether literature records indicated high ("abundant," "numerous"), medium ("fairly common," "not uncommon"), or low ("scarce," "rare") population density. Letters within the symbols indicate the locality (A—Alaska or Arizona, B—British Columbia, C—California or Colorado, I—Idaho, M—Montana, N—New Mexico, O—Oregon, W—Washington or Wyoming). Vertical dashed lines indicate years ending in "3"—the approximate peak year for the grouse-hare cycle. Solid lines connect symbols in instances of a definite population change described in the reference; broken lines connect symbols in instances of successive references to the same area by the same or different authors. See appendix, pp. 334–337.

Blue Grouse populations may be found. All references (see appendix) in the literature to the Blue Grouse which contained a concrete statement on relative numbers were plotted by species and by area (fig. 4). It is apparent that the data are too incomplete to warrant more than the most tentative conclusions. There are, however, several good descriptions of high grouse populations which suddenly were reduced.

Thus, for the race *D. o. obscurus,* Warren (1912:91) comments on the scarcity of both this species and the White-tailed Ptarmigan (*Lagopus leucurus*) in 1911 in north-central Colorado, where they had been common in 1909. Also Bailey (1928:197), discussing this race in New Mexico at the southern extreme of its range, indicates a fluc-

tuation in numbers from a low in 1916 through a high in 1922 and back to a low in 1927. By 1933, both Blue Grouse and ptarmigan had attained high numbers again (A. Starker Leopold, unpublished field notes).

To the north, in British Columbia, a series of observers documented the fall and rise in numbers of *D. o. richardsoni*. In the West Kootenay District, Kelso (1926:701) reports the species "common . . . until 1914, when its numbers were sadly reduced by a disease. It is regaining its former numbers [in 1924–25]." Ruffed Grouse were similarly affected. Mailliard (1932:274) states that *D. o. richardsoni* was "reported to have been quite common, but in 1928 grouse were very scarce" in the Kootenay Valley, about 50 miles from the area observed by Kelso. Ruffed Grouse were "even more scarce" than Blue Grouse. In another part of British Columbia, at Okanagan Landing, Munro (1919: 65) states that *D. o. richardsoni* was "abundant in normal years" but that their "numbers [were] greatly reduced during the past two years [1917–18]." In a later paper (1923:72) he indicates Ruffed and Sharp-tailed grouse suffered a decline at the same time, while snowshoe hares disappeared in 1915. Finally, Ferrie (*fide* Williams, 1954: 10) indicates that following a peak in 1942, populations of Blue Grouse and Sharp-tailed Grouse "crashed" in 1943.

Fewer convincing accounts of "crash" declines in the *fuliginosus* group exist in the literature. Howell (1917:186) says that *D. f. sierrae* in Mono County, California, was "well represented" in 1914, and very rare in 1917. Racey (1926:321) describes a situation at Alta Lake, British Columbia, in which the grouse (*D. f. fuliginosus* and *Canachites franklini*) were abundant in 1923 and almost gone in 1924. Fowle (MS) presents evidence from the annual reports of the British Columbia Game Commission which suggest a series of ten-year cycles from 1903 to 1943 in *D. f. fuliginosus* and snowshoe hares. Finally, observations at Sage Hen Creek, Nevada County, California, since 1951, indicate that there was an abrupt decline in *D. f. sierrae* in this area in 1952.

The Sage Hen Creek population.—Major objectives at the outset of the present study were to devise some way of determining the relative abundance of Sooty Grouse from year to year. Two techniques were employed, as previously mentioned: a count of displaying male grouse in the spring, and an analysis of the winter roost sites of the grouse. The validity of a census of displaying males rests upon the territorial behavior exhibited by adult male Sooty Grouse during the courtship period. The number of roost sites used in the course of a winter, and the amount of droppings accumulated beneath, presumably is dependent on the number of grouse that winter in an area. Granting this assumption, a count of winter roost sites and a measurement of the amount of droppings at these sites can serve as an index of the overwintering grouse population.

The method by which hooting males were counted has been described. Roost sites were located simply by cruising the entire study area, mapping and marking each tree or group of trees which was found to have grouse droppings. This was done primarily in early spring, when the melting snow pack made the droppings most conspicuous. It is estimated that well over 90 per cent of all the roost sites were found by this method, and certainly none of the major sites was overlooked.

The next step was to take samples of the droppings. The distribution of droppings beneath the roost trees was not random, that is, the droppings were grouped into discrete piles here and there beneath the trees of the site. Since it was desirable to determine approximately the total amount of droppings deposited each winter, a program of systematic sampling was adopted. At each site the number of dropping groups was first determined by inspection, then a circular area of one square meter was circumscribed around each area of greatest dropping concentration. The number of samples thus varied with the site, but the same number was always taken each year, allowing comparison

from year to year. The air-dry samples were then weighed to give a figure for the intensity of use for each roost site.

The results of these two index techniques are plotted on maps (fig. 2) for each year. Six cock grouse were found displaying in the spring of 1952, and a total of 109 roost sites was used in the preceding winter. The total weight of droppings collected was 2676 gms. In the spring of 1953, the number of hooting males decreased to two, each of which was in a site which had held a hooting cock in 1952. The number of roost sites used in the preceding winter decreased to 92, and the total dropping weight to 1548 gms. The spring of 1954 found two hooting males, again occupying the same two sites as 1953. The number of roost sites declined further to 51, but total dropping weight increased slightly, to 1595 gms. In the spring of 1955 no count of winter roost sites was made, but two hooting males were again present in the same two sites occupied by displaying males in the previous two years.

Table 1

Total Weight of Grouse Dropping Samples under Winter Roosts

Weight classes	Frequency of Class in 1952		1953		1954	
0– 9.9 gms.	65		59		29	
10– 19.9	17		15		3	
20– 29.9	7		3		3	
30– 39.9	5		5		4	
40– 49.9	0		2		1	
50– 59.9	2		1		1	
60– 69.9	3		2		3	
70– 79.9	1	7	0	5	1	6
80– 89.9	1		1		1	
90– 99.9	0		1		0	
100–109.9	0		0		1	
110–119.9	2		0		0	
120–129.9	0	4	0	1	0	3
130–139.9	1		1		1	
140–149.9	1		0		1	
150–159.9	0		1		1	
160–169.9	0		0		0	
170–179.9	2	4	0	2	0	2
180–189.9	1		1		0	
230–239.9	1		0		0	
250–259.9	0		0		1	
Total number of roosts used	109		92		51	
Total weight of droppings from all winter roosts	2676 gms.		1548 gms.		1595 gms.	

When the dropping samples are grouped by weight classes (table 1), it is seen that a significant decline in the frequency of the higher classes occurred between 1952 and 1953, and that between 1953 and 1954 the significant decrease was in the two lowest classes. Both hooting and roost site indices indicate a sharp decline in numbers of Sooty Grouse in 1952 and subsequent maintenance of a low population level (see also fig. 3). Since there is no open season in California, hunting was not a factor in the decline.

The occurrence of a sparse population of snowshoe hares (*Lepus americanus taho-*

ensis) in the Sage Hen Creek basin afforded the opportunity of determining whether the crash of the presumed ten-year cycle in Sooty Grouse also affected the hares, as would be expected. At the same time that winter grouse droppings were being sampled, the number of hare droppings present in each sample was recorded in the spring of 1952 and 1953. The average number of droppings thus represents an index of relative abundance of snowshoe hares in the preceding winter. In 1952 there was an average of 11.21 droppings per sample for 227 samples. In 1953, an average of 6.41 droppings per sample was present in 163 samples. The decline in average number of hare droppings per sample between 1952 and 1953 parallels the sharp decline in the Sooty Grouse population over this same period and suggests that the sparse snowshoe hare population may have declined synchronously with the grouse.

The evidence available on grouse and hare populations at Sage Hen Creek thus points to a sharp decline in numbers of both species in 1952. This decline falls into the schedule of the hypothetical ten-year cycle, which predicted a peak around 1951–53, followed by "crash" decline of continental grouse and hare populations (Rowan, 1950).

The accumulated data seem to indicate that Blue Grouse *may* resemble other species of northern grouse in exhibiting a ten-year cycle. As in these other grouse, a tendency for Blue Grouse populations to fluctuate synchronously with other grouse in a given area, and with snowshoe hare populations, is indicated by various comments in the cited literature. Local variations in the time of the crash decline are also apparent from the observations in British Columbia (Munro, 1919, 1923; Kelso, 1926).

One further point should be made with regard to "cycles." Some evidence suggests that population fluctuations in Blue Grouse, and perhaps other grouse, are less pronounced in the humid coastal forests bordering the north Pacific than in the interior. Buckley (1954:338) states that grouse, ptarmigan and snowshoe hare populations in southeastern Alaska are apparently relatively stable. Bendell (1955*a*:200, 221) found a population of Sooty Grouse at stable density on their breeding range from 1950 through 1953. In contradiction to this, Fowle (MS) documented a regular ten-year cycle in Sooty Grouse in coastal British Columbia, but he found that after 1935 the populations did not fluctuate markedly. He attributed the relative stability to changed habitat conditions on the summer range resulting from widespread forest fires and subsequent development of a favorable vegetational succession. It is possible that the stability noted by Buckley and Bendell is a fairly recent development, although perhaps not necessarily due to the causes suggested by Fowle.

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SUMMARY

Observations on the behavior of a small, semi-isolated population of Sooty Grouse at Sage Hen Creek, California, are compared with published observations on other populations. The grouse at Sage Hen Creek differ from most previously described populations in that they do not perform a seasonal altitudinal migration and in that no flocking behavior has been observed. These differences may be a reflection of low population density.

Evidence presently available points to pronounced differences in courtship behavior between the Dusky Grouse (*obscurus* group) of the interior and the Sooty Grouse (*fuliginosus* group) along the Pacific coast. These differences appear to be correlated with differences in summer range chosen by the two groups. The tendency toward communal display with no obvious territoriality is found in Dusky Grouse on open summer range, whereas solitary display and strongly developed territoriality occurs among Sooty Grouse on more wooded summer range. Although the grouse at Sage Hen Creek occupy the extreme eastern portion of the range of the *fuliginosus* group, the population has maintained the pattern of courship display and breeding habitat preference found in the main populations of the *fuliginosus* group. They show no tendency to resemble the *obscurus* group of the Great Basin in these respects, although the topography and vegetation of the Sage Hen drainage makes such a shift in habits theoretically possible.

The occurrence of displaying male grouse in the spring, and of winter roost sites, was determined at Sage Hen Creek for the period from the winter of 1951–52 through the spring of 1955. These two indices of population density suggest that the numbers of Sooty Grouse on the study area, and the numbers of snowshoe hares as well, declined in late 1952. This decline is perhaps of the same nature as other declines in Blue Grouse populations described in the literature.

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1929. On *Dendragapus obscurus obscurus*. Auk, 46:111–113.

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1952. A natural history survey of the Manning Park area, British Columbia. Occ. Pap. B. C. Prov. Mus. No. 9, 130 pp.

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1944. Food habits of blue grouse. Condor, 46:112–120.
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APPENDIX

References to Relative Numbers of Blue Grouse. Consult literature cited for publication and pagination of those references that are cited by year only.

Fuliginosus Group

Southeastern Alaska, British Columbia

Bailey, A. M. Auk, 44:1927:1–23, 184–205. Southeastern Alaska: In 1920–21, "common."

Bendell (1955*a*). Vancouver Island, B.C.: In 1950–53, "extremely high."

Bishop, L. B. N. Amer. Fauna No. 19, 1900:47–100. Yukon region: In 1899, "told that [sooty] grouse were common"; *Canachites* "reported as common"; *Bonasa* "rare at Lower Lebarge . . . common near Rampart City."

Brooks, A. Auk, 40, 1923:217–224. Porcher Island, B.C.: In 1920, "common" [implies they would be abundant, except for bald eagles].

Cook, F. S. Canad. Field-Nat., 61, 1947:131–133. Queen Charlotte Islands, B.C.: In 1942, "rather scarce in recent years."

Darcus, S. J. Canad. Field-Nat., 44, 1930:45–49. Queen Charlotte Islands, B.C.: In 1927, "very common on Graham Island . . . almost exterminated on Langara Island by domestic cats."

Grinnell, J. Univ. Calif. Publ. Zool., 5, 1909:171–264. Southeastern Alaska: In 1907, "common."

Hardy, G. A. Prov. Mus. Nat. Hist. Anthrop., Rept. for 1954, 1955:24–63. Vancouver Island: In 1943 and 1950–54, "common."

Jewett, S. G. Murrelet, 23, 1942:67–75. Southeastern Alaska: In 1941, though reported as "fairly common, . . . not a single grouse seen."

Patch, C. A. Canad. Field-Nat., 36, 1922:101–105, 133–136. Queen Charlotte Islands, B.C.: In 1919, "fairly common."

Racey (1926). See text. Large increase in number of great horned owls noted during grouse decline.

Swarth, H. S. Univ. Calif. Publ. Zool., 7, 1911:9–172. Southeastern Alaska: In 1909, "abundant."

Swarth, H. S. Univ. Calif. Publ. Zool., 10, 1912:1–124. Vancouver Island, B.C.: In 1910, "common at most of the points visited."

Willett, G. Condor, 16, 1914:71–91. Southeastern Alaska: In 1912–13, "hardly . . . abundant [but] very generally distributed." Goshawks common in 1912, very scarce in 1913.

Washington, Oregon, California

Anthony, A. W. Auk, 3, 1886:161–172. Washington County, Oregon: In Feb., 1884–June, 1885, "abundant." *Bonasa* "abundant."

Barlow, C. Condor, 2, 1900:103–110. Pyramid Peak Area, California: In 1900, "hear quite commonly."

Barlow, C., and Price, W. W. Condor, 3, 1901:151–184. Placerville–Lake Tahoe area, California: "not common at any point" prior to 1900 [1895?–1900].

Burdick, A. W. Condor, 46, 1944:238–242. Northern Cascade Mountains, Washington: In 1942, "abundant." *Canachites* "common."

Burleigh (1929). Coastal northwestern Washington: In Sept., 1919–June, 1920, "fairly plentiful." *Bonasa* "fairly plentiful."

DeGroot, D. S. Condor, 36, 1934:6–9. Echo Lake, California: In 1933, "seemed to be unusually abundant."

Ferry, J. F. Condor, 10, 1908:30–44. Yollo Bolly Mountains, California: In 1905, "common in favorable localities."

Fisher, A. K. N. Amer. Fauna No. 7, pt. II, 1893:7–393. Southern Sierras, California: In 1891, "nowhere common." *Centrocercus* also scarce.

Gabrielson, I. N. Condor, 33, 1931:110–121. Rogue River Valley, Oregon: "not common, [but] more common in 1926 than in other years."

Howell (1917). See text.

Jewett, S. G. Condor, 18, 1916:74–80. Tillamook County, Oregon: In 1911–14, "fairly common." *Bonasa,* "not uncommon."

Jewett, Taylor, Shaw, and Aldrich (1953). Mount Adams, Washington: In July, 1942, "very scarce."

Johnson (1929). Mount Rainier, Washington: In 1926, "saw the Sooty Grouse seldom in other parts of its natural range," but fairly common around one camp ground.

Kellogg, L. Univ. Calif. Publ. Zool, 12, 1916:335–398. Northern coast ranges, California: In 1911, "abundant . . . . A farmer . . . complained that grouse were so numerous that they were injuring his young grain."

Kobbé, W. H. Auk, 17, 1900:349–358. Cape Disappointment, Washington: In 1898, "only one seen." *Bonasa* not "abundant."

Lawrence, R. H. Auk, 9, 1892:39–47. Grey's Harbor, Washington: In 1890–91, "common." *Bonasa* "common."

McAllister, T. H., Jr., and Marshall, D. B. Auk, 62, 1945:177–189. Lake County, Oregon: In 1943, "common."

Merriam, C. H. N. Amer. Fauna No. 16, 1899:1–169. Mount Shasta, California: In 1898, "fairly common."

Merrill, J. C. Auk, 5, 1888:139-146. Fort Klamath, Oregon: In Sept., 1886–Aug. 1887, "generally distributed, . . . but not abundant." *Bonasa* "common."

Rathbun, S. F. Auk, 33, 1916:357–370. Olympic Mountains, Washington: In 1915–16, "fairly common." *Bonasa,* "not common."

Ray, M. S. Auk, 20, 1903:180–193. Central Sierras, California: In 1901–02, "not uncommon."

Ray, M. S. Auk, 22, 1905:363–371. Central Sierras, California: In 1903, "one seen . . . a few heard [in June]."

Stone, W., and Bunnell, A. S. Proc. Acad. Nat. Sci. Phila., 56, 1904:576–585. Mount Sanhedrin, California: In 1899, "numerous."

Townsend, C. H. Proc. U.S. Nat. Mus., 10, 1887:159–241. Mount Shasta, California: In 1883–84, "common."

Obscurus Group

British Columbia

Brooks, A. Auk, 20, 1903:277–284. Cariboo District, B.C.: In 1900–01, "common." *Canachites* "abundant."

Ferrie (*fide* Williams, 1954:10). See text.

Kelso (1926). See text.

Mailliard (1932). See text. High juvenile mortality noted during grouse decline.

Munro (1919). See text. Decline attributed to "cold, wet springs and the ravages of an intestinal parasite."

Munro (1923). See text. During decline, broods were "unusually small although there has been a fairly dry hatching season."

Munro, J. A., Occ. Pap. B. C. Prov. Mus. No. 8, 1950, 90 pp. Creston region, B. C.: "Blue Grouse were scarce in 1947 and only slightly less so in 1948 and 1949." *Bonasa* "scarce both in 1947 and 1948."

Rand, A. L. Nat. Mus. Canad. Bull. No. 105, 1946, 76 pp. Yukon region, B. C.: In 1944, "not common."

Rand, A. L. Canad. Field-Nat., 64, 1950:214–220. Yukon region, B. C.: In 1919–20, "scarce and local." *Bonasa, Canachites,* and *Lagopus* apparently also scarce.

Swarth, H. S. Univ. Calif. Publ. Zool., 24, 1924:315–394. Skeena River, B. C.: In 1921 "in small numbers." *Bonasa* "abundant."

Swarth (1926). Atlin region, B. C.: In 1924, "fairly common at high altitudes." *Canachites* "ordinarily . . . a common species . . . but in 1924 . . . had declined in numbers to a point of actual scarcity."

Oregon, Washington, Idaho, Montana, Wyoming

Arvey, M. D. Condor, 51, 1949:98. Custer and Blaine counties, Idaho: "much more numerous [in 1948 than] in 1938–44." *Canachites* "abundant."

Burleigh, T. D. Auk, 38, 1921:552–565. Lincoln County, Montana: In 1920, "a scarce breeding bird." *Bonasa* "common."

Gabrielson, I. N. Auk, 41, 1924:552–565. Wallowa County, Oregon: "past four years [1919–23?], . . . common [but] not exceedingly abundant." *Bonasa* "very common."

Hand, R. L. Condor, 43, 1941:220–232. Shoshone and Clearwater counties, Idaho: "In August, 1934, 150 seen at one time."

Jewett, S. G. Auk, 26, 1909:5–9. Baker County, Oregon: In 1906–07, "abundant." *Bonasa* "common."

Jewett, S. G. Condor, 14, 1912:191–194. Saw-tooth Mountains, Idaho: In 1910, "common."

Marshall, W. H. Condor, 47, 1945:170–172. Elmore County, Idaho: In winters of 1938–39 and 1939–40, "rather common." *Bonasa* "fairly common."

Merriam, C. H. N. Amer. Fauna No. 5, 1891:1–108. South-central Idaho: In 1890, "abundant."

Neilson (1926). Laramie Peak, Wyoming: In 1925, "most common."

Richmond, C. W., and Knowlton, F. H. Auk, 11, 1894:298–308. South-central Montana: In 1890, "very common."

Rust, H. J. Condor, 17, 1915:118–129. Kootenai County, Idaho: In 1910–14, "fairly common." Bonasa, "more abundant during . . . 1914 than for many years past."

Saunders (1914). Teton, and Lewis and Clark counties, Montana: In 1911–13, "abundant."

Saunders, A. A. Condor, 17, 1915:109–115. Flathead Lake, Montana: In 1914, "really common."

Snyder, J. O. Auk, 17, 1900:242–245. In 1894, "abundant." *Bonasa* "commonly seen."

Wing, L. Murrelet, 25, 1944:3–8. Okanogan County, Washington: In 1940, "most abundant."

Yocom, C. F., and Yocom, I. G. Murrelet, 27, 1946:10–12. Kootenai County, Idaho: In 1943, "reported as rather common, yet we did not see any." *Bonasa,* "rather common."

Colorado, Arizona, New Mexico

Bailey (1928). See text.
Drew, F. M. Bull. Nuttall Ornith. Club, 6, 1881:85–91, 138–143. San Juan County, Colorado: In 1879–80, "common." *Lagopus,* "very common."
Henshaw, H. W. Auk, 2–3, 1885–86:326–333, 73–80. Upper Pecos River, New Mexico: In 1883, "not abundant, though generally distributed."
Huey, L. M. Wilson Bull., 48, 1936:119–130. White Mountains, Arizona: In 1933, "not common."
Mitchell, W. I. Auk, 15, 1898:306–311. San Miguel County, New Mexico: In 1898, "common."
Rockwell, R. B., and Wetmore, A. Auk, 31, 1914:309–333. Golden, Colorado: In 1909, "not common."
Warren (1912). See text.

Museum of Vertebrate Zoology, University of California, Berkeley, California; current address, Department of Zoology, Montana State University, Missoula, Montana; January 24, 1956.

INTEGRATING MECHANISMS OF WINTER FLOCKS OF JUNCOS

By WINIFRED S. SABINE

In two earlier papers (Sabine, Physiol. Zool., 22, 1949:64–85; Condor, 57, 1955: 88–111) observations have been reported which suggest that the social activities in winter of the Slate-colored Junco (*Junco hyemalis*) and of the Oregon Junco (*Junco oreganus*), when studied by means of marked individuals, involve an orderly but rather complex type of flocking. The significant point is that although the migrant individuals which are to become winter residents arrive irregularly over a period of several weeks, they somehow manage to form themselves into distinct, stable winter flocks with mutually exclusive foraging territories. It is the intent of this paper to indicate the mechanisms which appear to bring about this result.

Materials and methods have been described in the papers cited. Wild, free-living birds, conspicuously marked for individual identification, were used in these studies. Two marked flocks of Slate-colored Juncos were observed by attracting them to a feeding station in Ithaca, New York. One marked flock of Oregon Juncos was studied at Deep Springs, California, and another at Seattle, Washington. A third marked flock of Slate-colored Juncos was observed in Ithaca in 1953. The results of this last study (unpublished) were corroborative of those obtained in the four preceding studies. In all instances the feeding stations were observed from an indoor post.

These five runs of observations were made on two species, and one of these doubtless included two races. The behavior patterns consistently displayed in flocking were, however, in all five flocks so closely in agreement as to be indistinguishable. This does not mean that each run of observations included all the data. On the contrary, new facts were constantly presented as conditions varied. Circumstances limited the number of times that the following important phenomena could be observed. (1) The build-up of the winter flock from the beginning of the fall migration was observed only at Deep Springs; the Seattle work was started in December. In Ithaca, for some reason not understood, the fall migrants do not visit the feeding station, although the spring migrants do so. The first juncos to appear there in November or December are already in an organized flock. (2) The behavior of the banded adults surviving from the flock of the year before was observed in Ithaca. There was no opportunity to study flocks of *Junco oreganus* in the same place for two successive years. In view of the similarity of the flocking patterns in five flocks, it is assumed that the patterns involved in the early development of the flocks and in the role of the experienced adult also are similar.

The junco flock is an association of birds which is firm in the identity of the individuals associated. It is therefore a socially segregated group. It is also spatially segregated. In a given small area a single group will be seen and no other. The formation of firm associations and the occupation of definite foraging areas take place at once among the earliest arrivals; it becomes obvious as soon as the first migrants are marked. The late comers are integrated into existing groups. The flock thus formed does not fly about as a unit, however. There appears to be no limit to the size of a foraging group. It may include the whole flock or it may consist of a single bird. The entire flocking procedure is marked by the continual forming and dissolving of groups of unpredictable size consisting of individuals that consort together and are daily visitors at the feeding sites.

It is especially to be noted that each bird shows its ability to fly about or perch, forage, and rest in solitude. This is an enlightening modification of the tendency to join fellow members, because it indicates that each bird has an independent knowledge of the limited environment it frequents.

In seeking the mechanisms on which this pattern of mutually exclusive flocking territories depends, there are certain possibilities that may be ruled out. (1) Since solitary foraging is observably not uncommon, there can be no leadership. Each individual knows independently the foraging territory of the flock. (2) Members of different flocks show no hostility to one another such as might produce a barrier between flocks. Although members of a flock keep to their feeding areas on the whole, this tendency does not rigidly control behavior. Individuals, usually alone, sometimes visit other flocks. During a long period of heavy snow in Seattle, birds not belonging to the occupant flock frequently visited the feeding station and were marked; they disappeared when the snow thawed (Sabine, 1955, *op. cit.*). In this interflock visiting, intruders did not meet with hostility on the part of members of the occupant flock; the latter were not even consistently dominant to the intruders. In fact, the intruders had a normal stability of rank in the pecking order. These two possibilities being excluded, it appears that the mechanisms which keep the flock together must be sought in forms of individual behavior operating uniformly within the flock. Such behavior arises, of course, from the environmental, social, and internal stimuli to which the birds respond.

The most obvious among these are the environmental stimuli which attract the juncos to their characteristic habitat—to localities under or near trees, to "edge" situations or open wooded areas.

Almost equally obvious are the responses to social stimuli. Clearly the junco is attracted by fellow members of the species and spends most of its time with its fellows. Two comments, however, must be made concerning the social responses of the species.

It has been noted that occasionally the social attraction lapses, and an individual forages and rests in solitude. In such cases it may be presumed that stimuli to which the bird responds in maintaining vital activities such as eating, resting, or exercising are temporarily in conflict with social stimuli and lead it either to leave its group or to remain behind when the latter departs. It is possible also that another drive is sometimes operative in the solitary junco. Such a bird has been observed many times to eat more slowly and in a relaxed posture, sitting back on its "heels," but it straightens up, eats faster, and hops in the normal restless manner when companions arrive. There may be an internal drive to be alone.

The stable winter flock is composed of birds which recognize each other at the distances maintained in foraging together. This conclusion rests on observations designed to force the birds to approach each other closely enough to stimulate pecking and thus show their rank in the pecking order. Food was offered exclusively on small trays (1 foot square or 1 by 1.5 feet). An incoming junco usually perched on the brush-pile and looked down at the line of trays. It was notable that the bird could withhold an immediate feeding reaction while it hopped along the brush surveying the situation. If the incoming bird was subordinate to all but one of the birds occupying trays, its reaction was predictable: it would go to the tray occupied by its subordinate. This predictable response to a complex stimulus-situation can be explained only on the supposition that the incoming bird recognized all of the individuals on the trays. Are the birds able, however, to recognize each other as individuals, visually or by call-notes, at longer range? If so, is a familiar group a more powerful social stimulus than a strange one? If these questions could be answered affirmatively, the capacity to recognize individuals would be one of the integrating mechanisms of the flock. Unfortunately there are no observations bearing on such a discriminatory response. The suggestion that it exists is merely a somewhat plausible speculation.

Among responses to internal stimuli, the exploratory drive of the junco shows two aspects that seem to be especially relevant to their flocking behavior. First, their feeding

is selective in the sense that they return repeatedly to certain spots. Within a day after being marked, at Deep Springs, recent migrant arrivals which later proved to be members of the stable winter flock were observed to be making repeated visits to the feeding station, and also to three natural unbaited sites. It is no doubt true that through trial and error learning they selected spots where an abundance of food reinforced the original stimuli; this was evidently true at the feeding station. However, in the case of the unbaited sites it can hardly be supposed that there were not unvisited spots "just as good" as those selected. Second, the feeding spots selected fell into a relatively limited foraging area or circuit; the sites known were not more than 200 or 300 yards apart. The flock was regularly observed only within this foraging circuit; the birds showed no tendency to range at random over large areas of the ranch. This flocking pattern suggests that the junco tends to develop routines and to move in an environment within which it has familiarized itself. Such a drive would be an important factor in shaping the flocking behavior.

This characteristic behavior of the junco was thrown into relief by the contrasting behavior of 12 House Finches (*Carpodacus mexicanus*) marked at the same time and place. Several of these were never seen again. Some were seen in parts of the ranch farther from the feeding station than any of the junco sites. One visited the station once in mid-winter, and one visited the station regularly throughout the entire winter, coming as often as the juncos and frequently with them, and continuing in the spring after the juncos departed.

It is obvious that the integrating mechanisms described above—attraction to a special kind of habitat, social attraction to their own species, and a tendency to routinized circuits—though indispensable to explaining the pattern of junco flocking, are still not sufficient to explain the distinctive feature of that pattern. This, as has been noted, is the two-fold fact that each individual junco can and does forage alone over the flock's circuit and that all the members of the flock forage over the same limited circuit and in the same feeding spots. Evidently an additional factor is needed to explain the segregation shown by the flock, and there is some evidence to indicate that this factor is the presence in a winter flock of a percentage of migrants which have survived from the previous year. Such adult homing birds, there is reason to suppose, start at once to visit areas familiar to them. Unfortunately the writer was not able either at Deep Springs or in Seattle, to observe flocks of Oregon Juncos in two successive years. The data which suggest that the behavior of the homing adult is a critical factor in enabling a population to become segregated into flocks are based on studies of the Slate-colored Junco.

At Ithaca, when there had been no feeding station the preceding year, the juncos first appeared as a flock in the edge of the woods during snow storms: that is, when the station had not been operated in previous years and there were therefore no banded homing birds familiar with the station, the flock was late. This occurred three times, in 1946, 1951, and 1953. In the fall of 1947, 1954, and 1955, when the feeding station had been operated in the preceding years, banded adults returned. Three characteristics distinguished their behavior. (1) Each year these banded birds appeared with the first group of juncos that arrived at the feeding station. In one instance a banded bird alone was the first junco seen. (2) The dates of their first appearance were earlier than the date for the appearance of junco flocks in years when the feeding station was not operated the preceding year. The banded individuals appeared in two instances in mid-November and in the third on December 3 and 4, whereas in other years the junco flock appeared in late December. (3) The feeding station in Ithaca is open lawn and needs large heaps of brush and evergreens for perching places and cover in order to attract juncos from the "edge" situation about fifty feet away. The banded birds came to the

site, however, even though it had not been thus equipped and would not normally attract a junco. In one instance, in 1947, even before food was provided at the station, three banded birds (from a flock of 14 in 1946) repeatedly visited the site, sometimes accompanied by a small number of unbanded birds. In 1954, although food was provided, there was no dense cover. Yet at least three banded adults (out of a flock of nine from the preceding winter) and an unknown number of unbanded birds used the station for the entire winter. No birds were banded in 1954, but at least two banded birds appeared in 1955 which must have survived from the banding of 1953. At their first appearance, food was provided but no cover or brush, and so long as this condition continued not more than four birds were seen at one time, and these invariably included two banded individuals. As soon as a brush heap was installed, the flock increased immediately to at least 16. When three small red pine trees were added for dense cover, the flock increased at once to more than 30. The promptness of this developmnt was probably aided by a snow storm.

The influence of the old birds on the inexperienced birds of the year does not need any particular explanation. The old birds go about their routes with the firmness that seems to attach to familiarization. The young birds, already endowed with tendencies to restrict their movements and to select and frequent definite areas and to join fellow members, have only to follow the old birds in order to develop the familiarity they seek. There are evidences that at the beginning of a season this process does not instantly work out to perfection. In the group of birds marked earliest at Deep Springs there was occasional absenteeism from the feeding station which did not occur later, and in the case of one bird about two weeks elapsed between the time when it was marked and the time when it became a regular member of the flock (Sabine, 1955, *op. cit.*). It seems that, granted the presence of a few homing adults, the operation of ordinary responses observed to be common to the species is sufficient to explain how all individuals come to frequent the same foraging territory and thus create the segregated flock.

Since the winter flocking pattern is a controlling influence in the activities of the winter resident juncos, its possible biological value might be conjectured. There seem to be two functions which could run concurrently. First, it seems most obviously to be a spacing device which tends to distribute the population over the available suitable territory. Second, it suggests that a definite, well-experienced homing goal must be developed in the individual birds, analogous to the breeding territory with the nest, in order to focus the migratory flights. It seems possible that the young junco, flying over a varied land topography, is able in one experience to acquire a photographically correct picture of its flight, which is useful in reverse the following spring. However, it would appear that both homing goals require the attractiveness of limited familiar territory to control the flight. The long activities of the breeding season provide this familiarity for the spring migration and the organization of the winter flock for the fall migration.

Ithaca, New York, February 15, 1956.

THE MOLT AND TESTIS CYCLES OF THE ANNA HUMMINGBIRD

By FRANCIS S. L. WILLIAMSON

At the present time, there is virtually no information in the literature on hummingbirds concerning the relation of the reproductive cycle, molt cycle, and other physiological events to the occupation and defense of territory. Consequently, the associated displays, and their function and relation to territorial occupation, are at best only partly understood. Moreover, any analysis of behavior should include a study of environmental relations of the species throughout the year in conjunction with the sequence of events in the annual cycle (Pitelka, 1942:196).

Among North American hummingbirds, the Anna Hummingbird (*Calypte anna*) offers several advantages for a study of these problems. It is permanently resident in most of its range, being confined as a breeding species to the Upper Sonoran Zone of California west of the Sierra Nevada and of northwestern Baja California (Grinnell and Miller, 1944:219). Field observations can therefore be made at any time of the year in the various situations utilized by this species, and specimens can be collected regularly for the study of the molt and testis cycles. In addition, a number of specimens are available in collections, and the existing literature is perhaps more extensive for this hummingbird than for any other in North America.

The primary objective of this study was to correlate the timing of events in the annual cycle of the male, particularly molt and reproduction, with the complex territorial behavior shown by this species. In particular, information was gathered on the nature of the territory in the non-breeding season, since none of any consequence has yet been reported in the literature. Information on behavior and display of Anna Hummingbirds is to be presented at a later date (Williamson and Pitelka, MS).

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MATERIAL AND METHODS

The data on territoriality and related behavior were obtained by field observation, from the spring of 1953 through the winter of 1954–55, in the Berkeley Hills on the east side of San Francisco Bay, California. Sixty-six specimens were collected in that area in the fall, winter, spring, and summer of 1954–55, for the study of the molt and testis cycles. In addition, specimens in the Museum of Vertebrate Zoology, California Academy of Sciences, and Stanford Natural History Museum were examined in the study of molt.

Two areas were used for the study of territory. One, a summer and fall feeding area,

is situated in the University of California Botanical Garden on the west side of the Berkeley Hills. The second, a winter and spring breeding area, is located in Tilden Regional Park on the east side of the Berkeley Hills. Although these areas are separated by only a short distance, they differ considerably in features of physiography and vegetation.

THE ANNUAL CYCLE

The Anna Hummingbird is a permanent resident throughout most of its range. However, it varies in abundance and activities in any particular location in a given part of the year. This applies particularly to the breeding season as contrasted with the season of subsidence of territorial activity, molt, and movement to favorable feeding areas in the dry part of the year.

The winter and spring months, from December to June, form the period in which the males are in reproductive condition and are occupying breeding territories. In the Berkeley Hills, the birds are found at this time in areas of broken chaparral, very frequently mixed with broad-leafed woodland of open character. They may also be found in riparian situations with willows and mixed shrubs predominating. The territories established consist of two distinct elements: (1) the core area, or primary territory, and (2) the buffer zone, or secondary territory (Pitelka, 1951*b*:644). The core area forms the center of activity of the male and contains one or more perches, usually on high stems, from which the male can observe in any direction about him. The majority of the songs, frequent chases, and all display flights originate at these perches. Chases of other birds, usually other hummingbirds, extend out over the buffer zone and often well beyond its boundaries out of view. Chatter and song usually accompany these flights as well as the more or less circular announcement flights made over the buffer zone. The breeding display and the dive display were rarely seen outside the core area.

The core area averages approximately one-fourth acre in size and occasionally is twice as large. The buffer zone varies in size and its limits are not easily defined. Pitelka (1951*b*:644), whose terminology of these areas is here adopted, estimated the size of the combined core area and buffer zone at six to ten acres.

Both of these areas are vigorously defended during the breeding season while the core area, or an area of similar size, is defended throughout the year. I have no records of one area being occupied continuously from one breeding season to the next, but such records are available (Pitelka, *loc. cit.*).

A male is usually promptly replaced when a territory is vacated, in some instances by a neighboring male and in others by a male not known earlier to have been in the vicinity. Frequent encounters between neighboring males are commonplace and each male seems well aware of the location of nearby males. In fact, some of the previously mentioned circuitous announcement flights pass over neighboring territories, and chases accompanied with chatter result.

In general, the winter and early spring months are the time of the year when the males assume the most belligerent and hostile attitudes, defending a large area by means of frequent, prolonged chases, abundant song, and the display flights characteristic of this species.

In May and June the behavior of the males undergoes marked changes. Display flights become infrequent and eventually stop entirely in most of the males. Territorial activity consists primarily of short chases in and about the core area which itself declines in size at localities where large numbers of birds feed. Molt commences in the juvenal males in late May and in the adults in early June. Coincident with the decline of territorial behavior in adults and the inception of molt in both age groups there is extensive movement, from the dry brushy hillsides, to areas of favorable food supply

such as gardens and other places where suitable plants such as tree tobacco and *Fuchsia* can be found. In these areas small territories are defended for varying periods of time by both adult and juvenal males, the former being more successful in this activity. In such places the density of birds may be great. By mid-August, defense of these small territories constitutes only a fraction of the activity seen in the breeding season. Song may be delivered quite regularly for considerable periods, but chases are brief and comparatively infrequent. Display flights are virtually absent and are performed by certain individuals only. At this time two males may frequently be seen feeding within a few feet of one another with no overt signs of hostility.

With the conclusion of molt in some adults in late August and early September, chases become more frequent and tend to be longer. By late September and early October many birds have finished molting and appreciable development of the testes has taken place. The tempo of territorial activity shows little further change until late November and early December. At this time the majority of the males, both juveniles and adults, have completed the molt and the testes are coming into breeding condition. In this period the winter rains commence and, in the local areas where suitable food in the rainy season attracts hummingbirds in numbers, females become increasingly more conspicuous in the dense population of males. Display flights increase abruptly, typically after a major spell of rainy weather, and movement to a suitable breeding habitat begins. By mid-December some males are still in the last stages of molt but all are in breeding condition. By January all the males are well established on breeding territories.

The evidence for the information presented here, except where otherwise indicated, is from my own field observations. Various aspects of behavior are outlined and described in papers of Pitelka (1942 and 1951*b*) and Woods (1927 and *fide* Bent, 1940: 371–387), which the reader may consult for additional information.

THE MOLT CYCLE

One object of the study of molt was to ascertain the period in which it occurred and its relation to the testis cycle and to the events in the cycle of breeding behavior. As will be shown later, a detailed study of the sequence of feather replacement has enabled me to set up arbitrary molt stages representing intervals in the molt process, thereby making possible estimates of the time required for both postjuvenal and annual molts. In addition this detailed study has revealed certain interesting features in the replacement of remiges, rectrices, and the gorget of the male. The manner and timing of molt in these areas may be linked with certain changes in behavior, in particular the display activity of the males.

Molt of the females was also studied. Although other aspects of the annual cycle in the female were not investigated, the information on molt alone makes possible certain interpretations of behavior which would not otherwise be possible. The comparatively brief five-month period in which adult females are molting terminates in October. From that time on they arrive in increasing numbers in the territories of the males. As will be shown later, this early appearance of the females results in increased activity of the males and possibly influences recrudescence of the testis.

A survey of the literature has failed to reveal any detailed account of molt in members of the family Trochilidae. Wagner (1955) has reported on certain aspects of molt in several species and Aldrich (1956) has recently provided some data on molt in the Allen Hummingbird (*Selasphorus sasin*). It is hoped that these observations in combination with the results reported here may form a basis for comparison among members of the family.

The data on period of molt and sequence of feather replacement have been derived

by examination of 421 study skins. Of the total examined, 165 specimens were actually taken while in the period of the molt, and these form the basis of most of the results obtained. Although no detailed study of pterylography of *Calypte anna* was undertaken, clipped alcoholic specimens were compared with other species described in the literature to enable me to apply the descriptive terms which have been used previously. The method of description is patterned after that of Pitelka (1945) for jays of the genus *Aphelocoma*.

Pterylography.—The pterylography of *C. anna* does not differ significantly from that reported for *Patagona gigas* (Thompson, 1901), "*Trochilus moschitus*" (=*Chrysolampis moschitus*) (Nitzsch, 1867), or *Selasphorus sasin* (Aldrich, 1956). The most thorough study of trochilid pterylography and the only one suitable for comparative purposes is that carried out by Aldrich (1956). All references to particular feather tracts and regions thereof follow his terminology.

A comparison of *Calypte anna* with *Selasphorus sasin* reveals the following differences in pterylography. Aldrich describes a vestigial seventh secondary for *sasin* which is not apparent in *anna*. Moreover, he indicates a number of greater secondary coverts larger than the number of secondaries, and this is puzzling. *C. anna* has six secondaries and six upper greater secondary coverts. The iridescent red feathers of the throat extend onto the crown in *anna*, covering the entire frontal region of the capital tract, whereas in *sasin* these specialized feathers are confined to the throat area.

Age determination.—It was necessary at the outset to segregate juveniles from adults. In males there are conspicuous differences that make such segregation easy. In females the differences are not so marked and in a few instances it was impossible to determine the age of the birds accurately.

The juvenal male differs most markedly from the adult in the coloration of the head and in the form of the tail. Young have a varying number of the red feathers on the crown and throat, usually only a scattered few, and never the complete complement of the adult. Interspersed among these are feathers of greenish-brown color, a few of these nearly always persisting until the last stages of molt.

The tail is useful for age determination in the early stages of molt. In the juvenal male, it is similar to the tail of the female in being composed of broad feathers with three distinct color zones: a green or grayish-brown inner zone, a black middle zone, and a white tip on the outer two and sometimes the outer three or four pairs of rectrices. The female has more white; the tips are broader and the white zone occurs on more feathers. The rectrices of the adult male are bluish-black centrally and grayish-brown laterally with the inner two pairs primarily green. Furthermore, the rectrices of adults are more narrow and attenuate in form, the outer pair strikingly so. Inasmuch as the tail feathers are replaced before the completion of molt on other parts of the body, the tail is not useful as an age criterion in the final stages of molt. The tails of an adult male, an adult female, and a juvenal male are shown in figure 1.

The only reliable difference noted that could be used to segregate juvenal from adult females was the form of the secondaries. This is shown in figure 2. In juveniles, both male and female, these feathers are rounded distally whereas those of the adult are truncate, or are pointed centrally, being incised slightly on either side of the rachis to form a shallow "W." At least one or two secondaries are among the last feathers to be replaced, and therefore juvenal birds can be distinguished in late stages of molt. There is some overlap in the variation of this character in the two age groups primarily as a result of wear; and as mentioned earlier, no precise age determination could be made for some females.

There is a fairly constant difference between the juvenal and adult females in the

number of red feathers in the throat region, although this is not completely reliable as an age criterion. The adults generally have a substantial patch of these feathers present whereas the juvenal birds have few or, more commonly, none at all. Adults sometimes have only a few, however, and so they cannot be distinguished on this basis alone.

No differences were detected in females in the form or coloration of the rectrices.

Postjuvenal molt of the male.—There were 78 specimens in juvenal plumage available for examination, and 72 of these were found to be in some stage of molt. The speci-

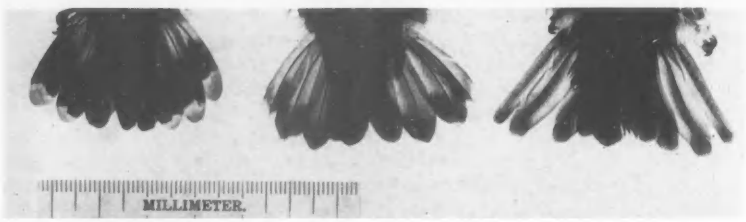


Fig. 1. Dorsal view of tails of adult female (left), juvenal male (center), and adult male (right) of Anna Hummingbird.

mens cover the entire period of molt and come from various localities in California, from Imperial, Los Angeles, and San Bernardino counties in the south to Sierra and Marin counties in the north. One specimen was taken in Pima County, Arizona.

Seven arbitrary stages of molt were defined after examination of the specimens (table 1). The sequence of feather replacement is consistent, and although some individual variation occurs in certain details in all areas examined, the general spread of molt over the body is orderly. The molt stages are plotted against time in figure 3.

No geographic variation in molt was found. Molt may begin as early as late May, and birds in the earliest stage of molt may be found as late as September. Molt in some birds continues into January and as some of these birds are in a middle or late-middle stage of molt, feather replacement undoubtedly continues in some instances into February. Thus, on a population basis, molt occurs over a period of eight to nine months.

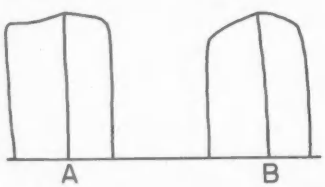


Fig. 2. Shape of outer secondaries in adult (A) and juvenal (B) Anna Hummingbirds.

That part of the period in which individual birds may be found in any stage of molt totals about four and one-half months. On the basis of the timing trend shown in figure 1, the postjuvenal molt in the individual is estimated to take approximately four and one-half months. In certain individuals there may be a retardation of molt in winter to the extent that it may require about six months. This view is supported by specimens in stage 5 collected as late as January.

The general sequence of the molt as well as its timing are summarized in table 1 and

figure 3. However, it is worthwhile to add to these condensed data remarks, first, on variation in the timing of molt over the body tracts and, second, on molt in the capital, alar and caudal tracts.

Spinal and ventral tracts. Molt begins in the sternal region of the ventral tract only slightly in advance of that in the anterior dorsal region of the spinal tract. Molt then progresses rapidly anteriorly and posteriorly in both of these tracts and spreads laterally more slowly. The ventral tract appears to be nearer completion at any given time, but both tracts may complete refeathering in the cervical region at approximately the same time.

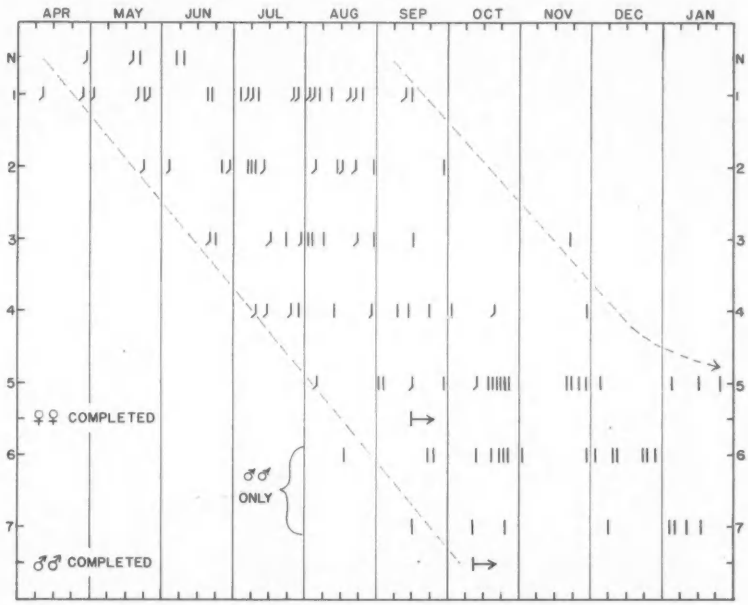


Fig. 3. Period of the postjuvenal molt in *Calypte anna*. Molt stages are described in table 1; N, no signs of molt; completion dates inferred from adults. Stages 6 and 7 apply only to males. Each female indicated by a hook at lower end of vertical line.

The interramal region of the ventral tract (gorget) does not undergo complete replacement until the molt elsewhere is complete or nearly so. At the time these feathers are dropped as a group, there may be a varying number of red gorget feathers already present. These specialized feathers evidently are replaced sporadically before and in all stages of the molt, and some recent ones may therefore be present when the overall molt of the face and throat occurs. These and the juvenal feathers of the region are replaced at one time. In a young male, one-third to three-quarters of the gorget may consist of red feathers at the time complete molt begins in the interramal region. Molt in this region coincides with molt in the loral, malar, and frontal regions of the capital tract as discussed below.

Capital tract. Molt begins in the coronal and occipital regions at apparently the same time and generally commences shortly after inception of molt on the body tracts. The replacement of the postocular feathers that form the greenish-gray line between the red of the crown and gorget is variable in timing, but occurs in the course of the refeathering of the coronal and occipital regions. The frontal, malar, and loral regions undergo complete replacement as a unit with the molt proceeding anteriorly. As with the gorget, a varying number of red feathers may be present at the time complete molt of

Table 1

Arbitrary Stages of the Postjuvenal Molt

Stage	1	2	3	4	5	6	7
Ventral tract	Feathers of sternal region breaking sheaths; scattered or no feathers ensheathed on cervical, axillar and abdominal regions.	Scattered to many feathers breaking sheaths.	Scattered to many feathers breaking sheaths.	Scattered feathers still breaking sheaths; ¾ replaced to molt complete.	Scattered feathers basally ensheathed in cervical region; in few birds, interramal region may be covered with pin feathers.	Growth complete except for interramal region.	Extensive molt in interramal region.
Spinal tract	Scattered or no feathers breaking sheaths in the anterior dorsal region.	Feathers breaking sheaths.	Feathers breaking sheaths in the cervical and posterior dorsal regions or cervical and anterior dorsal regions.	Scattered feathers breaking sheaths in dorsal and cervical regions; ⅔ replaced to molt complete.	Typically complete; scattered feathers may still be ensheathed in the cervical and posterior dorsal region.	Growth complete.	
Capital tract, dorsally	Scattered or no feathers breaking sheaths in the coronal and occupital regions.	Feathers of coronal and occipital regions breaking sheaths.	Feathers of coronal and occipital regions breaking sheaths.	Scattered feathers breaking sheaths in coronal and occipital regions; ½ replaced to molt complete.	Typically complete in coronal and occipital regions; in few birds, frontal area may be covered with pin feathers.	Growth complete except for frontal region.	Extensive molt in the frontal region.
Capital tract, laterally		Some feathers of postocular region may be breaking sheaths.	Feathers of postocular region breaking sheaths, or still old.	Molt complete, or scattered feathers of postocular region breaking sheaths.	Postocular region complete; in few birds the malar region may be covered with pin feathers.	Growth complete except for loral and malar regions.	Extensive molt in the malar region.

Table 1 (continued)

Stage	1	2	3	4	5	6	7
Primaries		1–4, 1–3, or 1–2 breaking sheaths; others old.	1–3, 1–4, or 1–5 fully grown; 6, 7, or 8-10 old.	1–6 fully grown; 7 breaking sheath to ¾ grown; 8–10 old.	1–8 fully grown, 9–10 old or incompletely grown.	Growth complete.	
Upper greater secondary coverts			Typically old; in birds molting secondaries they grade distally to proximally from ensheathed to ½ grown.	Typically molt complete; may still be breaking sheaths or old.	Growth complete.		
Secondaries			Typically old; molt may start when primary 6 is dropped; secondaries 1 or 6 or both breaking sheaths, 2–5 old.	1 and 6 new or in various growth stages; 2–5 old.	Variable; 2 to 4 secondaries new, others incompletely grown.	Typically complete; up to 4 old secondaries may still be present.	Growth complete.
Upper tail coverts		Typically old, 1–1 may be breaking sheaths.	Typically new; 1–3 ⅛ grown; 4–5 ¼ grown; or 1–1 pin feathers; others old.	Typically complete; may still be growing laterally.	Growth complete.		
Rectrices			Typically old; 1–1 or 1–1 and 2–2 breaking sheaths, or both pairs well grown.	1–1 and 2–2 dropped or incompletely grown; others dropped or old.	Typically pairs 1 and 2 fully grown, others old or breaking sheaths; or tail completely new.	Typically complete. Few birds have replaced 2 central pairs only.	

these areas commences. This phenomenon was noted by Woods (*fide* Bent, 1940:376), although the dates mentioned are misleading and no details are given.

Alar tract. The first feathers dropped are primaries 1–2, 1–2–3, or 1–2–3–4. The primaries molt in order until number 8 is replaced, and then primary 10 is dropped. This primary is always at least one-fourth and sometimes three-fourths grown, before primary 9 is dropped. Hence primary 9 is the last to be replaced. Primaries 9 and 10 are longer and more slender than the others in the series and undoubtedly are highly important in aerial maneuverability. Primaries 1 through 8 are always fully grown when primary 10 is dropped, giving the bird full use of the broad portion of the wing. Sequence of replacement of these two feathers is evidently related to the proper functioning of the outer margin of the wing, any impairment of which in the course of the molt is probably reduced by the precedence of 8 and 10, over 9.

The secondaries begin molt about the time primary 6 is dropped.

The greater primary and under primary coverts are replaced with the primaries.

When the first new primary or primaries are breaking sheaths, the marginal coverts begin replacement at the proximal side of the patagium. These coverts are completely new about the time primary 6 or 7 is fully grown.

The replacement sequence in the middle primary coverts is variable but always commences about the same time as that of the marginal coverts. The middle primary coverts may be dropped as a group or may be replaced more or less with the primaries, in both instances grading in development proximally to distally. The greater secondary coverts may begin molt with the primaries or may not begin until the primaries are one-half new. Molt of the secondary coverts precedes molt of the secondaries and they are usually fully grown when the secondaries begin molt. Exceptions occur, with one or two secondaries (1 and 6) being more or less ahead of the average growth stage among the coverts. I was able to discern that at least three out of nine birds commencing molt of the secondary coverts had secondary 1 or 6 or both well grown.

Caudal tract. Molt of the tail coverts begins when molt of the body tracts has proceeded posteriorly to the caudal area. These feathers drop as a unit and development of the incoming feathers proceeds most rapidly centrally. The replacement of the rectrices generally begins when primaries 1 to 6 are fully grown. At this time the tail coverts have completed development or may still be basally ensheathed. Although molt of the rectrices proceeds as in many passerines, from the central pair laterally, in this hummingbird some juveniles retain three or four lateral pairs of rectrices after the wing molt is complete. These may be retained for some time but they are always replaced before molt of the anterior portions of the head. The tail is replaced as two units with the two central pairs of feathers well grown or complete before the outer three pairs undergo replacement.

Postjuvenal molt of the female.—Forty specimens from various localities in California were available for examination, and of these 34 were taken in the period of molt. The arbitrary stages defined for the postjuvenal molt of males are applicable to the same molt of females. The early stages of molt in females involve additional loci, but these do not alter the timing of the molt. Stages 6 and 7, involving in the males molt of the red areas of the head, do not occur in the females. There are, in a few birds only, some deviations in the sequence of feather replacement not discovered in the males. These, however, are too slight and infrequent to justify establishing different criteria of molt progression in young females.

Molt may begin as early as the second week in April and birds in the earliest stage of molt may be found as late as the second week in September. The postjuvenal molt in individual birds is estimated to take approximately four months (fig. 3). Birds beginning to molt in September therefore do not conclude their molt until January.

Molt in juvenal females, then, occurs over a period about as lengthy as that for the juvenal males. However, from the plotting of the two groups in figure 3, it can be seen that there is a definite suggestion that postjuvenal molt begins and ends earlier in females than in males. This can be attributed in part only to the omission, in females, of stages 6 and 7; by reference to earlier stages it can be seen that as a group females are generally ahead of males.

In both males and females, the molt typically begins in the sternal region of the ventral tract. In the female, however, molt of this area is followed abruptly by the inception of molt in the interramal, coronal, anterior dorsal, and frontal regions, in the order given. In the male, as discussed earlier, there is no molt in the frontal and interramal regions until the last stages of molt are reached.

In addition, in the female, molt of the anterior dorsal region precedes somewhat any molt in the capital tract. The head of the female then undergoes complete feather replacement at the same time as the body tracts. In other respects the molt does not differ from that of the males.

I was unable to ascertain when the red feathers of the interramal region of the ventral tract are acquired. They do not appear in the months preceding the postjuvenal molt or are they acquired at the time of that molt. Virtually all adult females have at least a scattering of these feathers, which must therefore be acquired sporadically after the postjuvenal molt.

Two specimens were examined in which primaries 1 and 2 were fully grown, primary 3 was near completion, and molt in other areas had not commenced. These birds were assigned to stage 3, although there is reason to believe the body molt would be slightly delayed. Such variation is then reflected later, when, in both males and females, some variation occurs as to the time at which molt is completed on the body; it may be completed before or after molt on the alar and caudal tracts.

The postjuvenal molt of both sexes is complete.

Annual molt of the male.—Of 232 specimens examined, 45 were taken in some stage of the molt. Seven arbitrary stages of molt, defined after examination of the specimens, are summarized in table 2. No specimens were available that formed a second stage comparable to that described for the postjuvenal molt. This stage, involving a second activity in the primaries and inception of molt in the body tracts, is based on adult females. As with the postjuvenal molt, no geographic variation in timing or pattern of the annual molt was detected.

The general sequence of the molt and its timing are indicated in table 2 and figure 4, respectively. Molt may begin as early as the first week in June and, judging from the advanced condition of birds in later stages, even earlier. Refeathering of the head, the last stage in the molt, may occur as late as January. The period of time over which molt may be underway in at least some members of the population is eight months. The period of time estimated to be necessary for individual birds to complete the molt is two and one-half to three months. This estimate concerns molt exclusive of the red areas of the frontal, malar, loral and interramal regions of the head. All molt, except that of the red areas, is completed before replacement on these begins. The interval, if any, I was unable to determine. Assuming that the interval is negligible, and with most of the gorget requiring no more than 10 to 15 days for replacement, the total period of molt in the individual is three to three and one-half months.

The second and subsequent complete molts of the male differ from the postjuvenal molt in the following ways: (1) Molt commences in the alar tract with the dropping of primaries 1 and 2. Only one specimen is available in this stage; however, specimens in later stages agree in that their remiges were evidently at least partly grown before molt on the body began. In the postjuvenal molt, on the other hand, the ventral tract was the first area on the body to begin refeathering. (2) In adults, molts in the spinal and ventral tracts closely parallel each other, and in some instances the spinal tract may be slightly nearer completion at a given time. This contrasts with the situation in juvenal males. (3) In the adults the replacement of the rectrices always commences when primaries

Table 2

Arbitrary Stages of Complete Annual Molt

Stage	1	2	3	4	5	6	7
Ventral tract		Feathers breaking sheaths in sternal region.	Feathers breaking sheaths throughout tract.	Complete, or latest feathers breaking sheaths posteriorly and on neck.	Complete, or last new feathers breaking sheaths posteriorly and on neck.	Growth complete except interramal region.	Extensive replacement in the interramal region.
Spinal tract		Feathers breaking sheaths in anterior dorsal region.	Scattered feathers breaking sheaths throughout tract.	Complete, or latest feathers breaking sheaths in the posterior region.	Complete, or last new feathers breaking sheaths posteriorly.	Growth complete.	
Capital tract, dorsally		Feathers breaking sheaths in coronal regions.	Scattered feathers breaking sheaths in coronal and occipital regions.	Typically complete; scattered feathers may still be breaking sheaths.	Typically complete; scattered feathers may still be breaking sheaths.	Growth complete except frontal region.	Extensive replacement in the frontal region.
Capital tract, laterally		Feathers breaking sheaths in postocular region.	Scattered feathers breaking sheaths in postocular region.	Typically complete; scattered feathers may still be breaking sheaths.	Typically complete; scattered feathers may still be breaking sheaths.	Growth complete except malar and loral regions.	Extensive replacement in the loral and malar regions.
Primaries	1, 2 dropped.	1–2, 1–3 fully grown; 3, 4, 5 dropped, or 5–10 old.	1–5, or 1–6 fully grown.	1–7 fully grown, 8 dropped to nearly fully grown, 9 and 10 old.	1–8 fully grown, 9 old, dropped or growing, 10 dropped to fully grown.	Growth complete.	
Upper greater sec. coverts		Dropped.	Breaking sheaths.	Growth complete.			
Secondaries		Old.	1 dropped, old or breaking sheath, 2–5 old, 6 breaking sheath or fully grown.	1, or 1 and 2 fully grown; 3 old or breaking sheath; 4–5 old, 6 fully grown.	Variable. 1–2 or 1–3 and 6 fully grown; others old or incompletely grown.	Growth complete.	
Upper tail cov.		Old.	Breaking sheaths.	Growth complete.			
Rectrices		Old.	1–1, or 1–1 and 2–2 fully grown; others old.	1–1, 2–2 new, 3–3 old or breaking sheaths, 4–4, 5–5 old.	Pairs 1 and 2 fully grown; others in various conditions.	Growth complete.	

1-5 or 1-6 are fully grown. This timing may occur in the postjuvenal molt, or the replacement of rectrices may begin later.

Molt of rectrices in the adult usually begins with 1–1 and 2–2 emerging almost simultaneously, and the molt of the remaining rectrices usually proceeds rapidly. However, a slight interval is suggested between the first two pairs and the later ones, and it is of interest that the great delay that may occur in the young birds with the last three pairs of rectrices dropping near the end of the molt is reflected in the molt of the adult. Unlike the juveniles, there is no replacement of red feathers on the malar, loral, frontal,

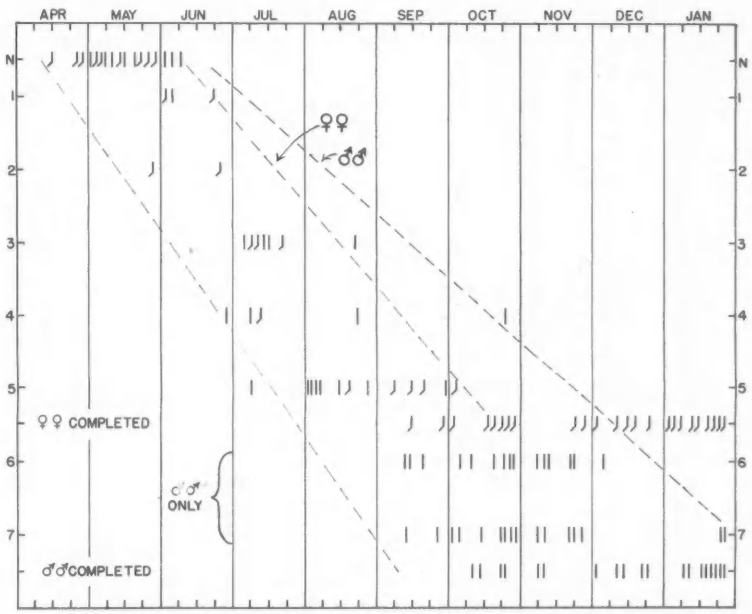


Fig. 4. Period of annual complete molt in *Calypte anna*. Molt stages are described in table 2; N, no signs of molt. Stages 6 and 7 apply only to males. Each female indicated by a hook at lower end of vertical line.

and interramal regions until molt on all portions of the body is complete. Adults proceed at this point to molt all the red feathers of the head, and this last stage is a very brief one. The head molt in adult and young males proceeds in similar fashion, that is, anteriorly. The sequence of feather replacement on the head is shown in figure 5. As previously indicated, the molt of adults lasts perhaps only three months as contrasted with the four and one-half months required for the postjuvenal molt.

Annual molt of the female.—Seventy specimens were examined, and of these only thirteen were taken in the period of the molt. The arbitrary stages defined for the annual molt of males are, with few qualifications, applicable to the molt of adult females. The early stages of molt involve the same additional loci on the head, discussed earlier for the juvenal females. Similarly, stages 6 and 7 do not occur. The only other variation noted is that from stage 3 on, usually in stage 5, some red gorget feathers are acquired

by the adult female, whereas in the immature ones, red feathers are apparently acquired after the regular molt. The dates for molt stages of the specimens are plotted with the adult males in figure 4.

Generalizations concerning period of the molt are difficult with such a small sample of specimens, but the molt apparently begins in early June and no birds in the earliest stage of molt were found after the third week in June. One specimen was in the final stage of molt in early October and several comparable ones were taken in September. It is estimated that molt in the individual birds may take two and one-half months for completion. The minimum period of time in which molt may be taking place in at least

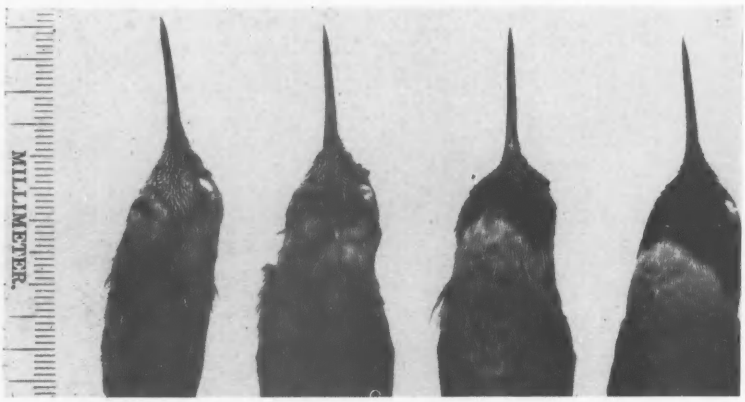


Fig. 5. Ventral view of heads of adult male Anna Hummingbirds arranged to show the sequence of feather replacement of the red gorget. Least advanced on the left; complete on the right. Note that molt proceeds anteriorly, the feathers at base of bill being replaced last.

some members of the population is five months. In light of the eight-month estimate for adult males it seems probable that this period is longer. As in the juvenal females there is an indication that the adult females may molt earlier as a group than the adult males.

As mentioned above, the annual molt of the adult female differs from that of males only in the molt of the head and in timing. In females this molt differs from the postjuvenal molt of the same sex only in the lack of activity in the interramal region late in the period.

Discussion.—The long period of nine months over which young of the year may be found in postjuvenal molt evidently reflects the long breeding season of the Anna Hummingbird. In one locality, Santa Barbara, this species may commence nesting activities in late December and continue until mid-June with two or possibly three broods per season (Pitelka, 1951*a*:198).

The time interval between fledging and the inception of postjuvenal molt is not known but this period appears to be lengthy. Young of the year are found in molt as early as mid-April and these may be presumed to be young from the first nestings. It is possible to estimate this interval more precisely by considering the late nestings and the birds most delayed in molt. If the presumed time necessary for postjuvenal molt, four and one-half months, is correct, and the last birds are fledged in June or early July, then at least two, and possibly three, months may elapse before molt begins. In addition.

retardation of the molt process may take place as evidenced by the following observations: (1) records of stage 5 in January; (2) the lengthy period sometimes necessary for full replacement of the body tracts; (3) the retention by some birds of several pairs of rectrices after most individuals have replaced these feathers; and (4) the fact that no birds were found in stage 1 later than September. Such retardation, whether it occurs on a significant scale or only occasionally, may be related to changes in food, qualitative or quantitative, in the course of the fall and early winter. It has been observed in the field that the birds congregate at this time about favorable food sources and the juvenal males are less successful than adults in maintaining feeding territories.

The molt of adults is similar in most respects to that of the juveniles. The molt of adults is briefer, being completed in three to three and one-half months in males and three months in females. It commences in the alar tract, whereas in the juveniles it commences in the ventral tract.

An estimate of 60 to 70 days for completion of molt in apparently several species is suggested by Wagner (1955:286). He did not attempt to separate sex and age groups, hence his results are difficult to evaluate. Further, Wagner reports for several species that molt begins in the alar tract, but again he fails to make a distinction between the postjuvenal molt and the annual molt of adults.

In males, over the anterior region of the head, parts of the capital and ventral tracts form the gorget and red crown, and these molt independently of the non-gorget portions of the same tracts. In females, on the other hand, there are additional loci on the head, and head feathers are replaced at the same time as body feathers. Some molt may occur in these regions in juvenal males before and in the course of the molt prior to the stage when the full complement of gorget feathers is acquired at or near the end of the molt. Wagner (1955:290) reports simultaneous replacement of iridescent feathers of the capital tract in *Eugenes fulvens,* but he does not mention whether this coincides with molt of the iridescent interramal region on the specimen he describes, as is true in *Calypte anna*. Further, he cites this as an "extreme" case rather than as a highly specialized mode of replacement, which is normal at least in *Calypte anna* and very likely in many other hummingbirds.

A strikingly different sequence of replacement of the contour feathers is discussed by Wagner (*loc. cit.*) for several species. He describes molt of the body tracts as beginning in the tail region toward the end of the molt of the rectrices and remiges. Replacement then proceeds anteriorly, terminating in the capital tract. I suspect that careful examination of a large series of specimens of any one of these species would reveal that this is not true.

The specialized head molt of the males is evidently related in timing to the onset of breeding occurring at the end of the molt period. The gorget, used in aggressive and breeding display, thus appears late in fresh, brilliant condition, and there appears to be a significant relation between completion of molt of this critical area and the consequent deferment of display behavior in any quantity until molt is completed.

There is a consistent irregularity in molt of the primaries in that the order of replacement is 1–8, 10, 9. This is apparently an adaptive device whereby aerial maneuverability is reduced to a minimum degree in the course of the molt. A somewhat similar phenomenon is noted in the molt of the tail with the central two pairs of feathers well grown or complete before molt of the outer three pairs commences. A similar sequence of primary replacement is reported by Wagner (1955:288) for *Calothorax lucifer*. In addition several modes of replacement for secondaries and rectrices are described by him for a number of species.

The inception of molt in the adults coincides with the close of the breeding season

in June when the days are nearing the longest of the year, and the dry season, with its associated scarcity of food, is well underway. The steady rise in mean monthly temperature and the decrease in amount of rainfall at this time of year are shown in figure 8. These, in combination with the changes in the light cycle, would seem to render very difficult, without experimental work, the discernment of the external factor, or factors, responsible for initiating the molt cycle. However, over the large geographic range occupied by this bird, the least variable climatic factor would seem to be the light cycle. Temperature and rainfall differ considerably from north to south in California. As mentioned earlier, it was recognized in the course of the study that the timing of molt inception and progression could not be linked with geographic location.

In June, also, the territorial behavior of the males is already undergoing marked changes through reduction in both the incidence of display flights and the size of the area defended (Pitelka, 1951*b*:645). There is a movement of large numbers of birds to areas of favorable food supply where small feeding territories are maintained for varying periods of time. Display flights are infrequent and performed by certain individuals only. Chases are short and relatively infrequent. The young males take part in this postbreeding dispersal and relocation but do not have the success of adults in maintaining feeding territories for any appreciable length of time.

Molt is generally completed prior to the onset of breeding activity in December and January when males were collected on breeding territories. The testes of both young and adults come into breeding condition in late November and early December although molt is still incomplete in some birds. Some adult males that are entering this period of breeding activity are still in one of the two last stages of molt and may remain so into January. In my records this is true of three out of 31. First-year males may be in any of the last four stages of molt at the beginning of the breeding season. This is true of 18 out of 49 records.

THE TESTIS CYCLE

It has been clearly indicated by earlier studies (Bent, 1940; Pitelka, 1942; Wagner, 1945; and others) that knowledge of the reproductive physiology of hummingbirds is a necessary prelude to an understanding of the complex territorial behavior of these birds.

An effort has been made to correlate certain events in the reproductive cycle with the climatic variables of day-length, temperature, and precipitation. In view of numerous attempts at such correlations for various passerine species, a comparison of some of these with the Anna Hummingbird seems desirable. Such a comparison is of interest in that this hummingbird is a north-temperate species breeding through the winter and spring, the males coming into breeding condition before the winter solstice.

As this study is primarily designed to develop correlations with behavior, emphasis is placed on the time relations of the reproductive cycle. No attempt has been made at detailed histological analysis. Specialized studies of the histology of the testis have been carried out for several species of passerine birds; a survey of this work is provided by Blanchard (1941) and by Blanchard and Erickson (1949).

The material for this study of the testis cycle consisted of 65 males collected from August, 1954, through September, 1955. The birds were skinned and the testes removed as promptly as possible following collection, usually within an hour. In some instances two to three hours elapsed before the gonads could be placed in a fixative. One bird was kept in a refrigerator overnight before the testes were removed. A comparison of histologic preparations from material fixed within 15 minutes and material not fixed for two to three hours revealed little difference. A similar comparison and finding is reported by Bullough (1942:167). The material was then treated in the following manner: fixa-

tion in Bouin's solution; dehydration in dioxane or alcohol; infiltration and embedding in paraffin; sectioning at 7μ and 10μ; staining with Delafield's hematoxylin; counterstaining with eosin; and mounting in balsam. This is, in most essentials, the technique utilized by Blanchard and Erickson (1949) and renders the material adequate for comparison with a well-studied passerine bird.

Measurements were taken of the longest and shortest diameters of the larger of the two testes, usually the left. In most instances, the smaller testis of a pair was nearly equal in size to the larger one. Measurements were made with an ocular micrometer and calipers for the small and large testes, respectively. The volume of the larger testis

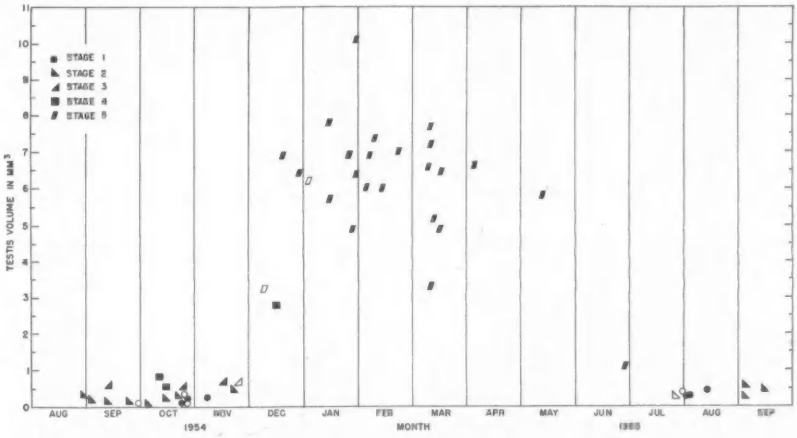
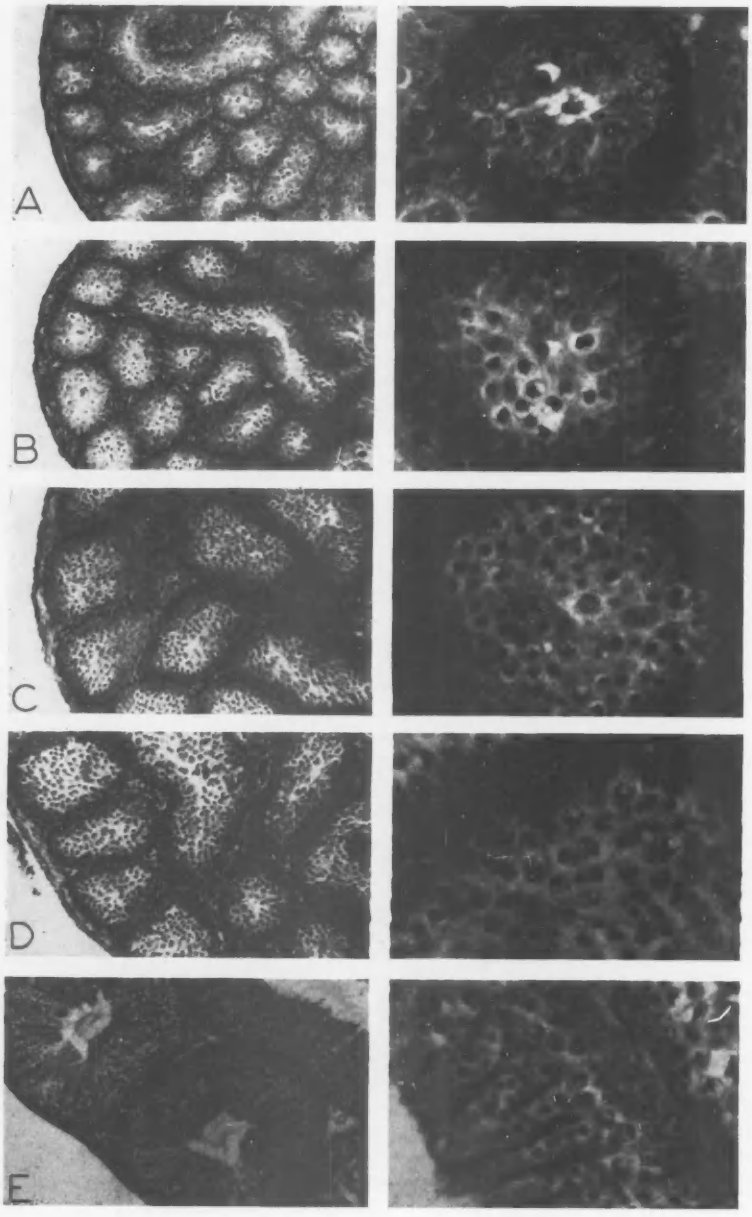


Fig. 6. The testis cycle in *Calypte anna* from August, 1954, through September, 1955. The solid and open symbols indicate adult and first-year birds, respectively. For definition of histologic stages see text.

was computed in cubic millimeters, using the formula for the volume of an ellipsoid, $V=4/3\ \pi ab^2$, where $a=\frac{1}{2}$ the longest diameter and $b=\frac{1}{2}$ the shortest diameter at the widest part of the testis. No weights were taken of any of the testes.

Histologic stages.—The histologic stages of the recrudescing testis in the Anna Hummingbird are, in most features, comparable to stages 3 to 7 described for the White-crowned Sparrow, *Zonotrichia leucophrys* (Blanchard, 1941). Stages 1 and 2 were not found and from the material available it is apparent that regression of the testes is not comparable to that in passerine birds inasmuch as no completely inactive state is reached. This might be suggested by the remarks of Wagner (1945:167–168) concerning the Mexican Violet-eared Hummingbird, *Colibri thalassinus*. Wagner states that some of the males of this species remain in the Valley of Mexico in the non-breeding season and that these birds "show all the exterior signs of readiness to breed, and the testes produce spermatozoa." Further he states that hummingbirds are capable of reproduction the greater part of the year except in the period of molt.

The testis stages and volumes are plotted against time in figure 6. The mean and extreme volumes for each histologic stage are shown in table 3. The juvenal males are included in both the table and the figure and in the discussion of the stages that follows.


A
B
C
D
E

The first-year males I collected showed no tendency whatever to be later than the adults in testis development.

A brief description of the histologic stages 1 to 5, approximately equivalent to stages 3 to 7 of Blanchard (1941), as they appear in *Calypte anna*, is as follows.

Stage 1 (fig. 7*a*). The tubules occupy the majority of the space within the testis and, although they are probably only slightly enlarged over the minimum size reached, each tubule contains two to four irregular rows of spermatogonia crowding toward the center. Many of these cells are dividing and a few appear to be degenerating. Primary spermatocytes are present in several of the tubules in each cross-section and occasionally one is seen in synapsis. There is usually no apparent lumen and an area of clear cytoplasm fills the center of the tubule. Two to four rows of connective tissue cells are present encircling the tubules. Functional interstitial cells are abundant, filling the triangles or corners where three or more tubules meet and they are also present in irregular rows between the tubules. Scattered blood vessels are found in the interstitial area. The tunica albuginea is moderately thin and only slightly fibrous.

Table 3

Volume Mean and Extremes for Histologic Stages 1–5

Histologic stage	Volume range	Mean volume	Number of specimens
1	.06– .34	.24	11
2	.14– .63	.34	12
3	.48– .66	.56	4
4	.59–2.81	1.42	3
5	1.13–10.15	6.14	25

Stage 2 (fig. 7*b*). The tubules now have enlarged so that they almost completely fill the space within the testis. Five or six rows of spermatogonia occupy most of the space within a tubule. Nearly all the tubules in a cross-section contain a few primary spermatocytes in that stage of synapsis where the chromatin is on one side of the nucleus. A small lumen is present in some of the tubules. When present, the lumen is bordered by a narrow area of clear cytoplasm. The connective tissue cells are reduced to one or two rows between the tubules. The triangles between the tubules are filled with functional interstitial cells. Scattered blood vessels are present in the interstitial area. The tunica albuginea has become noticeably thinner and more fibrous.

Stage 3 (fig. 7*c*). The tubules have continued to enlarge and the intertubular spaces are now very restricted in size. Three to five irregular rows of spermatogonia now appear as a margin in the tubule with the remainder of the space occupied by one to five rows of primary spermatocytes in synapsis. Scattered secondary spermatocytes and possibly a few spermatids border the center of some of the tubules. The lumen is not so conspicuous as in stage 2, but it appears in some of the tubules. One or two rows of connective tissue cells can be seen between some of the tubules. The markedly reduced intertubular triangles contain functional interstitial cells. Blood vessels seem more conspicuous in the interstitial area, and the tunica albuginea appears the same as in stage 2.

Fig. 7. Histologic stages in testis cycle of *Calypte anna*; figures at left × 125, at right × 500.

A. Stage 1, increase in spermatogonia and presence of first primary spermatocytes. Immature male taken October 24, 1954; molt stage 6, slight fat.

B. Stage 2, primary spermatocytes in synapsis. Adult male taken September 26, 1954; molt stage 7, slight fat.

C. Stage 3, predominance of primary spermatocytes in synapsis, and first appearance of secondary spermatocytes. Adult male taken October 24, 1954; molt stage 7, slight fat.

D. Stage 4, first appearance of spermatids. Adult male taken October 14, 1954; molt complete, moderate fat.

E. Stage 5, breeding condition. Adult male taken January 13, 1955; molt complete, slight fat.

Stage 4 (fig. 7*d*). The tubules are very enlarged and now occupy virtually the entire area of a cross-section. Spermatogonia are present in one to three or four rows forming a margin around the rim of the tubule. Primary spermatocytes are arranged in three to four irregular rows, and the now more apparent lumen is bordered by several rows of secondary spermatocytes and spermatids. In one specimen some bundles of mature sperm are present, in groups of seven to twelve, their heads pointing outward from the lumen. Some connective tissue cells are still apparent between tubules and functional interstitial cells fill the intertubular triangles. Blood vessels are conspicuous throughout the interstitial area. The tunica albuginea is thin and fibrous, very similar to its appearance in stages 2 and 3.

Stage 5 (fig. 7*e*). The tubules are now of maximum dimensions and contain one or two rows of spermatogonia, one to three irregular rows of primary spermatocytes, and seven to ten irregular rows of secondary spermatocytes and spermatids. The latter completely encircle the large lumen and can be seen in various stages of metamorphosis. The lumina contain bundles of seven to 12 mature sperm arranged radially, their heads pointing away from the lumen. The lumina of most of the tubules contain free sperm, and in all there are accumulations of cytoplasm cast off from the metamorphosing spermatids. Connective tissue cells still are apparent between a few of the tubules and functional interstitial cells are at a minimum. The latter can be found only occasionally in the triangles or corners between the tubules. Blood vessels are conspicuous in the interstitial area. The tunica albuginea is extremely thin, and the nuclei are difficult to see and are very much flattened.

Testis volume.—The general picture of volumetric increase is shown in table 4. It can be readily seen that the greatest increase in volume takes place in late November and early December at which time the males are commencing display activities and moving onto breeding territories. Prior to this time there is no consistent trend in the population. Birds may be found with testes in any histologic stage from 1 to 4, at least in the months of October and November, and each of these stages has testis volumes averaging greater than the preceding stage. The broad overlap that exists in testis volume in histologic stages 2, 3, and 4 can be seen in table 3.

The picture that results shows certain deviations from that reported for the Starling, *Sturnus vulgaris* (Bissonnette, 1930; Bissonnette and Chapnick, 1930; Bullough, 1942) and the White-crowned Sparrow (Blanchard, 1941; Blanchard and Erickson, 1949). In these two passerine birds, testis volume in the population shows a gradual and uninterrupted increase up to the time that stage 6 (here stage 4) is reached. There is then a rapid increase in testis volume that slows down somewhat after breeding condition is reached. There is naturally some overlap in volume of particular histologic stages but not to the degree shown in the Anna Hummingbird. For example, Blanchard and Erickson (1949:270) indicate stages 1, 2 and 3 overlapping in volume; the same is true for 3 and 4, and 4 and 5.

Testis volume is not a criterion that can be used to indicate histologic stage in the greater part of the cycle (table 4). Testes of 4 $mm.^3$ or greater in volume may be assumed to be in breeding condition, but for those that are smaller no assumption can be made. The volume increases in stages 1 to 4, shown in table 3, are detectable only through computed averages for a number of specimens.

The range of testis volume in any given stage may be great, as indicated in table 3. Bullough (1942:174), working with the British Starling, attributed this, at least in stages 6 and 7 (here stages 4 and 5), to age. He assumed that the very old males have smaller testes. In the British Starling first-year males do not breed and consequently the testes do not reach the maximum size of the adults. In *Calypte anna* there is in addition great variation in the histologic condition achieved by various individuals of the same age at any given time prior to their coming into full breeding condition.

Intertubular cells.—As is apparent from the preceding section on histologic stages, I have recognized only three categories of intertubular structures: (1) connective tissue cells, (2) functional interstitial or Leydig cells, and (3) blood vessels. These are the

interstitial constituents recognized by Bullough (1942:176) and are the only ones discerned in the course of examination of my material.

The numbers of all these structures, with the exception of blood vessels, seem to diminish in abundance as the tubules increase in size. The most striking decline is in numbers of functional interstitial cells. In stage 5 these cells are difficult to find and appear only scattered in the triangles between the tubules. Whether or not these cells actually become less abundant, or only appear to do so because of increase in size of other portions of the testis, I am unable to say.

Table 4

Testis Volume and Histologic Stage for 15-day Periods, August, 1954–September, 1955

Dates	Volume MM³ range	Average volume	Number of specimens	Histologic stages
Aug. 17–31	.35	.36	1	2
Sept. 1–15	.21– .66	.36	3	2–3
Sept. 16–30	.12– .18	.15	2	1–2
Oct. 1–15	.14– .86	.46	4	2–4
Oct. 16–30	.06– .48	.23	6	1–3
Oct. 31–Nov. 14	.21	.21	1	1
Nov. 15–29	.54– .59	.56	3	2–3
Nov. 30–Dec. 14	3.21	3.21	1	5
Dec. 15–29	2.81–6.93	5.40	3	4–5
Dec. 30–Jan. 13	6.23–7.85	7.04	2	5
Jan. 14–28	4.91–6.93	6.21	3	5
Jan. 29–Feb. 12	6.07–10.14	7.39	5	5
Feb. 13–27	6.00–7.09	6.54	2	5
Feb. 28–Mar. 14	3.39–7.76	5.91	5	5
Mar. 15–29	4.92–6.47	5.74	2	5
Mar. 30–Apr. 13	6.66	6.66	1	5
Apr. 14–28	.....	.....	....	....
Apr. 29–May 13	5.87	5.87	1	5
May 14–28	.....	.....	....	....
May 29–June 12	.....	.....	....	....
June 13–27	.....	.....	....	....
June 28–July 13	1.13	1.13	1	5
July 14–28	.....	.....	....	....
July 29–Aug. 13	.25– .42	.33	6	1–2
Aug. 14–28	.....	.....	....	....
Aug. 29–Sept. 12	0.34–0.63	0.48	2	2
Sept. 13–27	0.46	0.46	1	2

Discussion.—It can be seen in figure 6 and table 4 that there is considerable variability in the time at which any particular histologic stage is reached. This is especially interesting in view of the fact that all members of the population apparently come into breeding condition in a brief period of possibly two, and not more than three, weeks. In any event this was the situation in the fall of 1954 when this period covered the last week in November and the first two weeks in December.

In November, birds in histologic stages 1 to 3 were collected and birds in stage 4 were undoubtedly present as two in this stage were collected in October. Birds in stage 1 were collected as late as November 7, and birds in stages 2 and 3 as late as November 21. No additional specimens were collected until December 8, and from this date on, all those collected were in breeding condition with the exception of one male in late stage 4 collected on December 15.

The two males in stage 4 collected on October 10 and 14 indicate that some birds

can reach this advanced condition and remain so for an extended period of time. In passerine birds, stage 6 appears to be very brief with a prompt transition to breeding condition (Bullough, 1942:180; Blanchard, 1949:273).

It would seem, then, that a search for timing correlations between testis stages and environmental factors, which might be postulated to have an influence on the testis cycle, at least in the early stages of recrudescence, is of little purpose. There is an apparent lack of synchrony in the population in the autumn until that time when some factor, or set of factors, serves to bring the entire population into breeding condition at virtually the same time.

It was indicated in the section on molt that all the males collected were examined to determine the degree of feather replacement. This information was correlated with the stage of testis development and at least one interesting result is available. All the males in stage 4 had completed the molt and it would seem that the energy requirements of molt might have a direct effect on the rate of testis development. However, four other males that had completed feather replacement were in stages 1, 2, and 3. It may be, therefore, that completion of molt is a necessary prelude to early attainment of stage 4.

A system of classifying relative quantity of body fat was developed using the categories *heavy, moderate, slight* and *no* fat. Some of the birds were found to be completely encased in a jacket of fat but this apparently has no detectably consistent relation to either molt program or degree of testis development. Birds with slight, moderate, or heavy fat may be in any combination of molt and testis stages. The accumulation of fat deposits seems most likely connected with one of two possible sets of conditions: First, fat deposition may be linked with, and so preparatory for, the dry season of the year in late summer and early autumn and the paucity of food of that time. This shortage relates both to insects and nectar-bearing flowers, the primary foods. At this time of the year many individuals are molting, and the birds are moving about a great deal from one favorable locality to another. It would seem that the acquisition of fat at the onset of this critical period could be of distinct value in carrying the birds through the dry season. As indicated by Grinnell and Miller (1944:218), this situation has become less critical in recent years through the extensive planting of many non-native plants that flower abundantly in the period when native plants are quiescent.

The second possibility is that the birds are far less active from summer through the fall, and at least those fortunate enough to maintain feeding territories in favorable situations are more or less predisposed to becoming fat. This was true of all the males I collected in this interval. Activity was relatively scant and food was abundantly available in the particular area used as a source for my specimens.

It is apparent that the long reproductive period of the Anna Hummingbird, from December to June, covers the better part of the year, with the remaining interval occupied by molt. Even so, on a population basis at least, there is a varying degree of overlap of molt and reproductive activity both at the beginning and end of the breeding season.

CLIMATIC CORRELATIONS

The available data on histologic changes in the testes are not sufficient for any completely satisfactory correlations with annual climatic events. Only continued collection of material over a period of several years will produce results adequate for critical evaluation. However, some inferences as to the influence of climate on the breeding cycle can be deduced from my assembled data.

Temperature.—The monthly temperature data presented in graphic form in figure 8 can be easily contrasted with the data on testis development in figure 6. These give some indication of the relation of temperature to the recrudescing testes. It can be seen

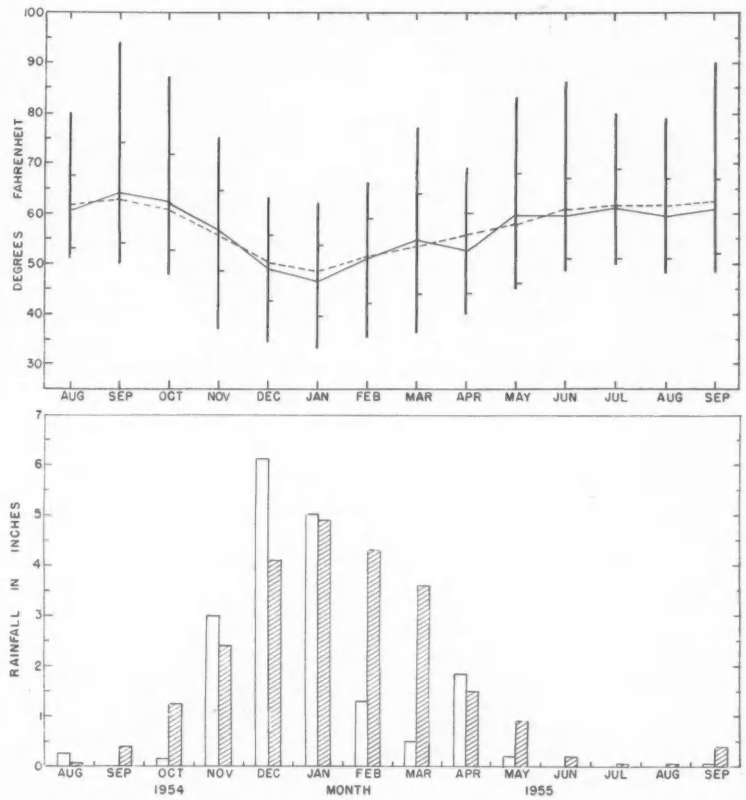


Fig. 8. Temperature and precipitation data for Berkeley from August, 1954, through September, 1955. Upper: Vertical lines represent temperature range (maxima, minima); horizontal lines indicate mean maxima and mean minima, for the month indicated. The continuous solid and dotted lines indicate mean monthly temperature during the study, and normal mean monthly temperature, respectively. Lower: Hollow and shaded columns indicate monthly rainfall during the study and normal monthly rainfall for Berkeley, respectively.

that recrudescence is in progress in the two warmest months, September and October, but that the greatly accelerated development of early December occurs while the temperature is declining. December, the first month when all the males collected were found in breeding condition, was only slightly warmer on the average than the coldest month of the year, January. The temperature then commences to rise and continues rising until the warmest month of the year, usually September.

Nesting commences in December and, for the population, probably reaches a peak in January and February (Pitelka, 1951*b*:648). These months are the coolest and generally the wettest of the year. This situation is evidently paralleled in some other species. For example, Skutch (*fide* Bent, 1940:452) makes some interesting comments concerning the nesting of the White-eared Hummingbird (*Hylocharis leucotis*) in very cool

weather in the highlands of western Guatemala. This species nests at or near the end of the rainy season, from October to December, when frequent frosts and cold winds prevail.

Precipitation.—The onset of heavy winter rains in November and December, shown in figure 8, seems to suggest a correlation with at least the terminal phase of recrudescence of the gonads. In the fall of 1954, the first substantial rains fell in the first 15 days of November with 1.47 inches recorded on November 15. There was an abrupt increase in territorial behavior following this initial heavy rain. No more precipitation was recorded until December, when rain fell nine out of the first ten days of the month. In this period, and shortly thereafter, the birds became established more or less promptly on suitable breeding territories and all males collected had mature sperm in the testes.

Again, Skutch (*fide* Bent, 1940:453) found that male White-eared Hummingbirds move to breeding territories and begin singing in the rainy season in August. The rain subsides in that area in October and flowering plants become more numerous. Breeding behavior then becomes more prominent. Cessation of breeding is coincident with the onset of the dry season in January. The cycle of breeding in *Calypte anna*, with regard to the rainy and dry seasons, is very similar. On the Pacific slope of southern Costa Rica, Skutch (*fide* Bent, 1940:435) found that several species of hummingbirds were breeding in the rainy season and early portion of the dry season when the nests of other birds were scarce. He also indicates that mountain inhabiting forms of hummingbirds in that area have breeding seasons that coincide with the rainy portion of the year.

Day-length.—Blanchard (1941:96–97) presents in graphic form the curve of variation in hours of daylight for Berkeley, and this can be referred to for particular information. It will suffice here to say that recrudescence of the testes begins sometime after the June solstice and continues, as the number of hours of daylight declines through the autumn. The birds come into breeding condition in late November and early December, before the winter solstice, when the days are approaching the shortest of the year.

Discussion.—The achievement of breeding condition seems more closely related to the onset of winter rains than to any other climatic factor. The number of consecutive days of rainfall appears to be of greater significance than the actual amount of rain received. Until further evidence is available it seems reasonable to assume that an inherent rhythm is operative in controlling the testis cycle, and that this rhythm is modifiable by rainfall and other factors, such as the presence of females, with the ensuing breeding season occurring in the period when food plants are most numerous.

It seems very probable that the presence of females has a modifying influence on testis development. I was able to detect a noticeable increase in activity of the males, including the performance of specialized displays, when females were present in the territories. Burger (1953:234), working with the Starling (*Sturnus vulgaris*), demonstrated that the presence of a female increases the magnitude of testis response by 45 per cent on given dates and under similar light conditions. Wagner (1945:171) believed the presence of female Violet-eared Hummingbirds caused increase in excitement among males.

Bené (1946:414–415), in discussing the Black-chinned Hummingbirds (*Archilochus alexandri*) is of the opinion that seasonal changes in light and temperature coincide with internal physiological rhythms regulating migration and initiating the breeding season. This is based only on the fact that migratory hummingbirds tend to reach the breeding areas in the period when flowering plants are available for food. This would not seem to be true of *Calypte anna*, or for that matter the many tropical, non-migratory forms.

SUMMARY AND CONCLUSIONS

An examination of the testis and molt cycles of the Anna Hummingbird has been coupled with year-long observations of territoriality and its associated behavior (fig. 9).

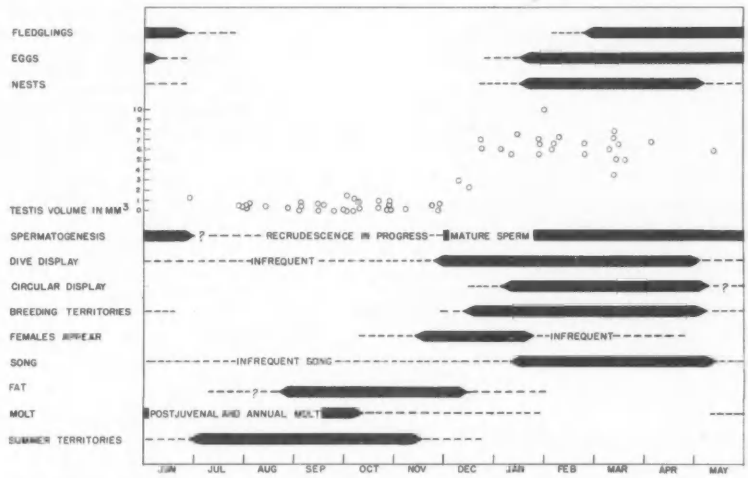


Fig. 9. Outline of general features of annual cycle of reproduction and behavior in the Anna Hummingbird. The solid bars indicate that the particular activity listed is in evidence; the dotted lines indicate a subsidence of the activity.

The molt of the males occupies a period from June to January, between breeding seasons. This process coincides with the dry season of the year and an associated paucity of food, at least in the normal or natural situation. During the molt males are relatively inactive, and many individuals become fat. The molt is modified to the extent that the feathers of certain areas critical in display and flight are replaced in a specialized manner at the end of the molt period. Molt in females is completed before that of males. Females then appear in increasing numbers in and about the territorial areas of the males, prior to the onset of breeding.

Recrudescence of the testes commences in the course of the molt period and is well underway in August. Testis development is not uniform in males. Some birds may reach the advanced condition of stage 4 while others are in various earlier stages of development. Regardless of this, all the members of the population come into breeding condition at approximately the same time, in early December. There is broad overlap of molt and the early stages of testis development, although molt is generally complete when the birds reach the breeding state. Recrudescence of the testes is probably influenced by a number of factors, including increase in winter rains and ultimate increase in food, the completion of molt, and possibly also the presence of females.

Territory size and defense vary according to the season of the year and the physiological condition of the males. During the dry season when the birds are molting, small areas are weakly defended. With an increase in testis volume, and a probable corresponding rise in hormone level, activity increases. When the breeding condition is attained, most of the males are established on large, actively defended territories.

The frequency and type of display undergo radical changes in the late fall as the breeding season approaches or begins. More complex displays appear and display in general is witnessed more consistently in that season. Many displays associated with defense of the small summer feeding areas are no longer seen.

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TWO NEW BIRDS FROM THE MIOCENE OF FLORIDA

By PIERCE BRODKORB

Although a large avifauna is known from Miocene deposits in western North America, only eight species have been described from this epoch in the eastern part of the continent. Four sea birds are recorded from Maryland, and one each is known from North Carolina and South Carolina (Wetmore, 1940). From the Hawthorne formation of the Lower Miocene of Florida a shore bird (Wetmore, 1943) and a chachalaca (Brodkorb, 1954) have been described. To these are added in the present paper a cormorant and a kite. The kite, referable to the Tertiary genus *Proictinia*, further strengthens the already marked resemblance of the Hawthorne fauna to the Lower Miocene fauna of the Great Plains.

Family Phalacrocoracidae

Phalacrocorax subvolans, new species

Type.—Proximal half of right humerus, no. 4500, University of Florida collection, from Lower Miocene at Thomas Farm, eight miles north of Bell, Gilchrist County, Florida. Collected by Robert S. Bader, spring, 1955.

Diagnosis.—Agrees with *Phalacrocorax wetmorei* Brodkorb (1955) in conformation of caput humeri and bicipital crest, but differs as follows: proximal width less; width of shaft less; ligamental furrow shorter and less deep; deltoid crest longer; internal tuberosity sharper and capital groove correspondingly deeper; bicipital furrow wider.

The great width of the bicipital furrow leaves a larger surface for the insertion of M. coracobrachialis anterior. This indicates that the present species was a better soarer than either the living cormorants examined or the fossil species in which this furrow has been adequately described or figured. It approaches the condition in the humerus of the darters (*Anhinga*), which customarily soar for long intervals.

Measurements.—Proximal width, 21.5; width through external and internal tuberosities, 20.1; width of shaft, 7.6; depth of head, 7.5; length of ligamental furrow, 10.0; length of deltoid crest, 40.3; width of bicipital furrow, 11.1 mm. Angle formed by external tuberosity and deltoid crest, 130 degrees.

The temporal and geographic distribution of the fossil species of *Phalacrocorax* is as follows:

Oligocene:

Phalacrocorax littoralis (Milne-Edwards, 1868). France.
Phalacrocorax miocaenus (Milne-Edwards, 1868). France.
Pha'acrocorax marinavis Shufeldt (1915). Oregon.
Phalacrocorax mediterraneus Shufeldt (1915). Colorado.

Miocene:

Phalacrocorax intermedius (Milne-Edwards, 1868). France.
Pka'acrocorax praecarbo (Ammon, 1918). Germany.
Phalacrocorax femora'is L. Miller (1929). California.
Pha'acrocorax subvolans Brodkorb. Florida.

Piiocene:

Phalacrocorax destefani Regalia (1902). Italy.
Phalacrocorax idahensis (Marsh, 1870). Idaho.
Phalacrocorax rogersi Howard (1932). California.
Phalacrocorax kennelli Howard (1949). California.
Phalacrocorax wetmorei Brodkorb (1955). Florida.

Pleistocene:

Phalacrocorax macropus (Cope, 1878). Oregon.
Phalacrocorax pampeanus Moreno and Mercerat (1891). Argentina.
Phalacrocorax gregorii De Vis (1906). Australia.
Phalacrocorax vetustus De Vis (1906). Australia.

The size of the new species is less than in *P. marinavis, P. intermedius, P. praecarbo, P. femoralis, P. rogersi,* and *P. gregorii.* It is much less than in the giant species *P. mediterraneus, P. idahensis,* and *P. macropus.* The new species is larger than *P. littoralis, P. destefani, P. kennelli,* and the dwarf *P. miocaenus.*

The caput humeri is more rounded and less produced than in *P. littoralis, P. miocaenus, P. intermedius, P. femoralis, P. destefani, P. gregorii,* and *P. vetustus.* The head is deeper than in *P. kennelli.* The margin of the bicipital crest is smooth, rather than dilated and undulating as in *P. littoralis, P. miocaenus,* and *P. femoralis.* The bicipital furrow is wider than in *P. littoralis, P. miocaenus,* and *P. kennelli.* The ligamental furrow is deeper than in *P. miocaenus.* The angle formed by the external tuberosity and the deltoid crest is wider than in *P. destefani* (120 degrees) and *P. vetustus* (125 degrees). It is less than in *P. gregorii* (135 degrees).

Fig. 1. Proximal half of right humerus of *Phalacrocorax subvolans.* × 1. Drawing by Esther Coogle.

Family Accipitridae

Proictinia floridana, new species

Type.—Distal portion of left tarsometatarsus, no. 777, Brodkorb Collection, University of Florida, from Lower Miocene at Thomas Farm, eight miles north of Bell, Gilchrist County, Florida. Collected by P. Brodkorb, March 21, 1954.

Diagnosis.—Agrees in general proportions with *Proictinia effera* Wetmore (1923) from the Lower Miocene of Nebraska. Differs as follows: distal foramen larger and located lower on shaft; trochlea for digit two less flaring from line of shaft and with its wing produced farther posterior; size smaller.

Measurements.—Dimensions in millimeters of the type of *P. floridana* are followed in parentheses by those of the cast of the type of *P. effera.* Width through trochleae, 8.8 (9.5); width of shaft through facet for first metatarsal, 5.5 (6.3 approx.); width of trochlea three, 2.5 (2.7); depth of trochlea four, 3.9 (5.1); maximum depth of trochlea two, 4.7 (not available for *effera*); height of foramen above

intertrochlear groove on anterior face, 1.5 (2.2); height on posterior face, 0.9 (not available for *effera*); vertical diameter of foramen, 1.3 (1.0).

I follow Wetmore in using *Proictinia* Shufeldt as the generic name for the small Tertiary kites. The type of the genus, *Proictinia gilmorei* Shufeldt (1913), is practically a *nomen vanum*, since it was based upon a fragmentary coracoid of an immature bird. Most of the other American accipitrids have been founded on metatarsi, so direct comparison with Shufeldt's species is not possible and the assignment of forms to this genus is by analogy only.

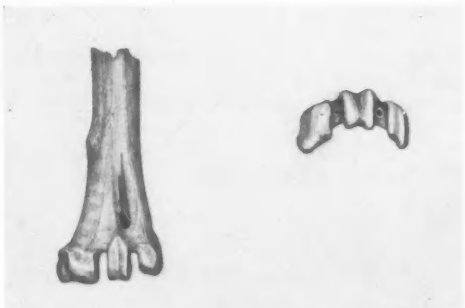

Fig. 2. Distal portion of left tarsometatarsus of *Proictinia floridana*. × 2. Drawing by Esther Coogle.

A cast of the type of *Proictinia effera* (Am. Mus. Nat. Hist. 6299) has been made available through the kindness of Mrs. Rachel Nichols. It is a complete right tarsometatarsus with associated phalanges but not, however, completely freed from the matrix.

The present species is the twentieth accipitrid to be described from American Tertiary formations and the first from east of the Mississippi. With the exception of the species of *Proictinia*, all other American Tertiary accipitrids are so much larger that no comparison is needed.

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RED-TAILED HAWK AND HORNED OWL POPULATIONS IN WISCONSIN

By GORDON ORIANS and FRANK KUHLMAN

In the winter of 1953 we began a three-year investigation of interactions between populations of the Red-tailed Hawk (*Buteo jamaicensis*) and the Horned Owl (*Bubo virginianus*) on 95 square miles of open farm land in southern Green County, Wisconsin. The study area included all of Sylvester and Jefferson townships and parts of Clarno and Monroe townships. Additional observations were made on land within one-quarter mile of the area since birds nesting there fed partly in the study area. In the three-year period 90 nests of Red-tails and 48 nests of Horned Owls were examined.

The original vegetation of the area, as determined from surveyors' records by Dr. J. T. Curtis, Department of Botany, University of Wisconsin, consisted of a tongue of maple (*Acer saccharum*)–basswood (*Tilia americana*) forest bordered on the east and northwest by a belt of oak-basswood (*Quercus-Tilia*) forest which continued across the north-central portion of the area. The southeast part and most of the northern edge of the area were covered primarily by tall grass prairie with small islands and extensions of the forest. Extensive agriculture has greatly altered this original vegetation so that only small woodlots remain (fig. 1). Maple-basswood has replaced the oak-basswood chiefly on the north slopes, but oak dominates the drier slopes. The prairie areas are still essentially treeless with only a few scattered fence-row willows (*Salix*), American elms (*Ulmus americana*), and black cherries (*Prunus serotina*) (fig. 2). The principal farm crops are corn, hay, and oats. Much of the land is in pasture.

The other avian raptors breeding on the area were Screech Owls (*Otus asio*), a few Sparrow Hawks (*Falco sparverius*), and Cooper Hawks (*Accipiter cooperi*). Broad-winged Hawks (*Buteo platypterus*), Sharp-shinned Hawks (*Accipiter striatus*), and Marsh Hawks (*Circus cyaneus*) visited the area during migration, and Short-eared Owls (*Asio flammeus*) were uncommon in winter. Rough-legged Hawks (*Buteo lagopus*), sometimes as common as Red-tails between mid-November and mid-April, were the only other large raptors on the area in any numbers.

The word "competition" has been used to refer to a confusing variety of relationships between individuals, but recently Andrewartha and Birch (1954) have given good reasons for restricting the use of that term. Therefore, in this paper we have adopted the following terminology: *Interaction*, any relationship among individuals of the same or differing species; *competition*, the demand of individuals upon any common resource which is in short supply; and *interference*, any detrimental interaction not falling into the class of competition as just defined.

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THE RED-TAILED HAWK POPULATION

Winter population.—Throughout the winter the Red-tails moved about considerably, often sitting and hunting in small groups. We encountered birds throughout the area but most frequently in the wooded portions. Rough-legged Hawks, on the other hand, were most common on the prairie areas.

Of considerable interest was the scarcity of immature Red-tails in the winter. From November 30, 1953, to February 15, 1954, we observed 39 adults and 10 immature

Fig. 1. Typical scene on study area showing small woodlots, scattered trees along a stream, and cropland.

birds. In a comparable period the following winter, we saw 36 adults and two immatures. Many immature birds may migrate to the Gulf coast, as we have three winter recoveries from this region of nestlings banded in Green County (table 1).

In early autumn we often saw paired birds over their nesting woods, but this was not observed in the winter. Yet Fitch, Swenson, and Tillotson (1946) found that California birds were paired and permanently resident in definite hunting and nesting territories. On our study area all resident birds were paired on their territories by the end of February and only migrants travelled singly or in groups.

Breeding population.—The huge, relatively flat nests of the Red-tail, built on large horizontal branches, often at considerable distance from the trunk, were easily located in winter and readily identified. We noted the location of all old nests in the winter since many of them would be repaired or new ones built upon their foundations.

New nests apparently were built in a few days. We observed birds building only twice. On January 30, 1952, we saw two birds carrying sticks to a nearly completed nest and watched building at another nest on March 6, 1954. Twigs used in new nests were obviously broken from larger branches, as the fresh ends were conspicuous. Corn husks were used as lining material in all nests we studied.

Although nests were sometimes built as early as late January, incubation did not start at such an early date. We flushed our earliest incubating bird from a nest on March 1, 1953. We found the first incubating birds in 1954 and 1955 on March 13 and 11, respectively. By aging the young at the time of banding and using an incubation

period of about 35 days (Hardy, 1939), we estimated that the first eggs were laid in the first week of March but that most of them were laid in the second and third weeks. Both sexes participated in incubation. Twice we observed the replacement of one bird by the other.

None of the nests under observation was used three years in succession by Red-tails, but ten nests were used two years in succession. Eight new nests were built in the same woods as the old one, and sometimes the Red-tails re-used a nest after it had remained

Table 1

Recoveries of Nestling Red-tailed Hawks Banded on the Study Area

Date banded	Date recovered	Place recovered	Age at recovery	Distance and direction from banding location
May 26, 1951	July 25, 1951	Monroe, Wis.	3 months	.....
May 10, 1952	Dec. 23, 1952	San Augustin Co., Texas	8 months	800 miles SSW
May 12, 1952	March 9, 1953	Brownview, Point Coupe Parish, La.	10½ months	850 miles SSW
May 2, 1953	Dec. 1, 1953	Jersey, Buchanan Co., Iowa	7 months	120 miles W
May 2, 1953	Nov. 3, 1953	Elgin, Kane Co., Illinois	6 months	80 miles SE
May 8, 1953	Aug. 10, 1953	Dakota, Waushara Co., Wis.	3½ months	110 miles N
May 9, 1953	Sept. 4, 1953	Basco, Dane Co., Wis.	4½ months	25 miles N
May 9, 1953	Dec. 27, 1953	Lake City, Columbia Co., Fla.	8 months	950 miles SE
May 23, 1953	Jan. 30, 1954	Evansville, Rock Co., Wis.	9 months	23 miles NE
May 6, 1954	July 27, 1954	Juda, Green Co., Wis.	2½ months	2 miles NE
May 20, 1954	July 13, 1954	Stevenson, Ill.	2 months	½ mile S
May 20, 1954	Dec. 7, 1954	Fairbury, Livingston Co., Ill.	7 months	120 miles SE
May 22, 1954	Sept. 3, 1954	Monroe, Wis.	3½ months	2 miles W

unused for one season. Often Horned Owls used the old Red-tail nests, and sometimes the two species used the same nest in alternate years.

Although elms were outnumbered by both sugar maples and white oaks (*Quercus alba*), 52 of the 90 nests we found were in elms, perhaps because these trees are common along streams and fence-rows, and because their large, spreading branches provide many suitable nest sites. We found 15 nests in sugar maples, 9 in white oaks, 6 in basswoods, 5 in willows, 2 in red oaks (*Quercus borealis*), and one each in burr oak (*Quercus macrocarpa*), black walnut (*Juglans nigra*), and cottonwood (*Populus deltoides*).

The height of 49 nests ranged from 30 to 90 feet and averaged 57 (±13.1) feet. Nine nests were enclosed by dense woods so that the adults had to fly through trees to reach them. Twenty-three were on the edges of dense woods with access from the open air to the nest (fig. 4*a*). Fifty-seven nests were situated in isolated trees or in open stands of four to several dozen trees with unobstructed access to the nest from several sides (fig. 4*b*). Because Red-tails will nest in such open situations, the prairie regions of our study area were inhabited by them (fig. 3).

In 1954 there were 33 nesting pairs and six non-nesting pairs (0.41 pairs per square mile), while in 1955 there were 27 nesting pairs and one non-nesting pair (0.29 pairs per square mile). Only after a careful search of the area and a study of the birds' behavior did we call pairs non-nesters. In the only other study of Red-tail populations known to us, Fitch, Swenson, and Tillotson (1946) report that in Madera County, California, the density was one pair per 320 acres, a population about five times as dense.

In warm weather food not eaten was removed quickly from the nest, but small bits

sometimes were trampled into the bottom of the nest and caused a considerable stench. Green branches were brought to the nest throughout the fledgling period. They may serve as a clean resting place for the nestlings.

The young, which leave the nest in early June, are dependent on the adults for an unknown period (fig. 5). Recoveries of banded birds shot by local farmers in late July may indicate that independent hunting has started by then (table 1).

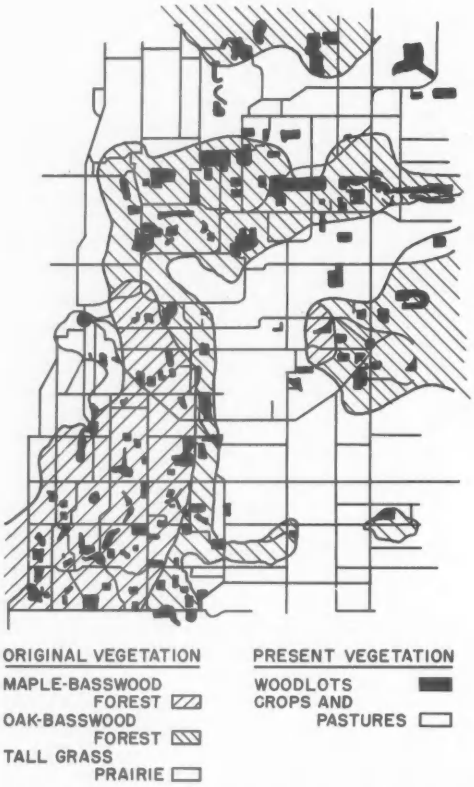

Fig. 2. Original and present vegetation on study area. Scale: 5 mm. = 1 mile.

Nesting success.—We consider a nest successful if one young bird is raised to an age when it can be expected to leave the nest. In 1953, 48 young were reared in 27 nests (1.8 young per nest): one bird in each of six nests, two in 12, and three in six; three nests failed. In contrast, only 36 young were raised in 33 nests in 1954 (1.1 young per nest): one young in each of seven nests, two in 13, and three in one; 12 nests failed. Of the 27 nests in 1955 (1.4 young per nest), four had one young, nine had two young, six had three, and eight failed, making a total of 40 nestlings reared (table 2).

Causes of nesting failure were difficult, and in most cases impossible, to determine. In the critical period when the nestlings were under two weeks of age, there was no

unusually cold weather in any of the three years, but weather may play an undiscovered role in causing nesting failure, as the Red-tail is not tenacious in its brooding. Our presence at one nest just before a sudden thunderstorm caused one failure.

As the only two young we found dead in the nests had been dead too long for us to ascertain the cause, we have no direct evidence of nestling deaths from either starvation or disease. Populations of pheasants and cottontails, the two principal prey species,

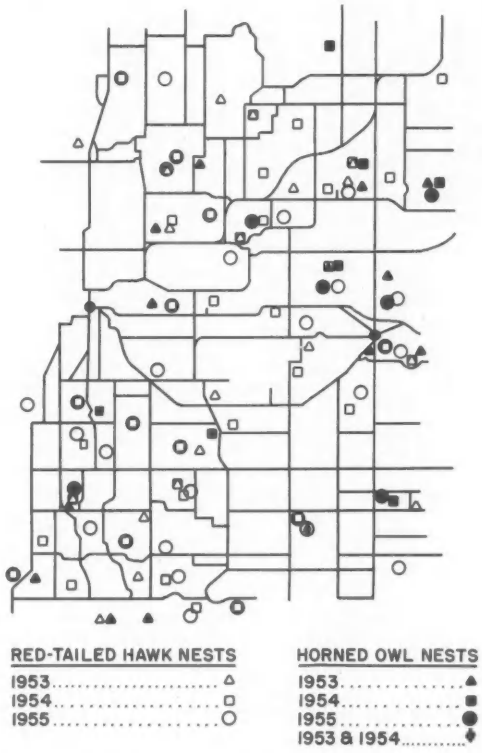

Fig. 3. Locations of nests of Red-tailed Hawks and Horned Owls.

showed no great fluctuations in Green County in the course of our study, according to Wisconsin Conservation Department hunting kill records (table 3). Of the three years, 1954 should have been the year of greatest prey-availability and yet this was the year of poorest Red-tail productivity.

While we have observed no evidence of direct Horned Owl predation on nestling Red-tails, we feel it is a possibility that should not be overlooked, as Hamerstrom and Hamerstrom (1951) report that a tethered fledgling Red-tail was killed by Horned Owls.

One nest failure of 1955 can be correlated with the death of one of the adults which we found shot beneath the nest.

Fitch, Swenson, and Tillotson (1946) attributed the nest failures in their study to

four known causes: desertion probably caused by the intrusion of the investigators; jays, which were observed robbing one nest and held responsible in another case; blood-sucking flies; and trampling by a parent which killed one nestling.

Table 2

Nesting Success of Red-tailed Hawks and Horned Owls

Species	Year	Number of pairs	Pop.* density	Number of nests	Failures	Young/nest 1	2	3	Average number young/nest	Aver. no. young/successful nest
Red-tailed Hawk	1953	....	.....	27	3	6	12	6	1.8	2.0
	1954	38	0.41	33	12	7	13	1	1.1	1.7
	1955	28	0.29	27	8	4	9	6	1.4	2.1
Horned Owl	1953	20	0.22	13	4	4	5	0	1.1	1.6
	1954	19	0.20	17	1	2	12	2	1.9	2.0
	1955	12	0.12	11	3	3	4	1	1.3	1.8

* Population density expressed as pairs per square mile.

Food.—Our food data for the Red-tail is based entirely on nest remains because pellets do not accurately represent the Red-tail food. In the nests we found: 46 adult Ring-necked Pheasants (*Phasianus colchicus*), 26 cottontails (*Sylvilagus floridanus*), 20 chickens, 9 American Crows (*Corvus brachyrhynchos*), 8 mice (*Microtus*), 6 thirteen-lined ground squirrels (*Citellus tridecemlineatus*), 5 Redwings (*Agelaius phoeniceus*), 2 meadow jumping mice (*Zapus hudsonius*), 2 Yellow-shafted Flickers (*Colaptes auratus*), 2 domestic pigs, 2 domestic turkeys, 2 short-tailed shrews (*Blarina brevicauda*), 3 meadowlarks (*Sturnella* sp.), 1 Cowbird (*Molothrus ater*), 1 Starling (*Sturnus vulgaris*), 1 Rock Dove (*Columba livia*), 1 gray squirrel (*Sciurus carolinensis*), 1 fox squirrel (*Sciurus niger*), and 1 frog (*Rana* sp.).

We found manure on the feathers of many of the chickens in the nests and believe, as do a number of local farmers, that Red-tails pick up dead chickens which are spread on the fields with the manure.

The variability of Red-tail food in southern Wisconsin is seen when our data are compared with those of Errington (1933:27). He found the following prey items in nests in southern and central Wisconsin: 49 thirteen-lined ground squirrels, 42 *Microtus,* 18 chickens, 18 cottontails, 11 arboreal squirrels, 5 *Blarina,* 4 *Peromyscus,* 4 snakes, and 3 eastern chipmunks (*Tamias striatus*). The most striking differences are the complete absence of pheasants, the most numerous item in our study, and the large number of thirteen-lined ground squirrels which Errington found. Green County is one of the best pheasant areas in Wisconsin and the Red-tails on our study area are fully utilizing this abundant food supply.

Red-tails in California eat more rodents and reptiles, and birds are apparently a minor item (Fitch, Swenson, and Tillotson, 1946). The following data from their paper are taken from a list of 625 prey items from 14 nests over a three-year period: 380 Cali-

Table 3

Estimates of Pheasant and Rabbit Kills in Green County*

Year	Pheasant kill	Rabbit kill
1952 (fall)	19,647	27,115
1953 "	20,424	34,625
1954 "	15,380	31,230

* From Wisconsin Conservation Department records.

fornia ground squirrels (*Citellus beecheyi*), 79 pocket gophers (*Thomomys bottae*), 62 cottontails (*Sylvilagus auduboni*), 13 wood rats (*Neotoma fuscipes*), 10 kangaroo rats (*Dipodomys heermanni*), 8 Merriam chipmunks (*Eutamias merriami*), 7 additional rodents, 23 birds, and 23 reptiles.

Plumage variations.—The Red-tailed Hawk is noted for its wide variety of plumages, particularly in the western portion of its range. On our study area no extremely

Fig. 4*a*. Red-tailed Hawk nest in a red oak (*Quercus borealis*) on the edge of dense woods.

Fig. 4*b*. Red-tailed Hawk nest in a basswood (*Tilia americana*) on the edge of an open, heavily grazed woodlot.

white individuals have been observed, but we saw black individuals on ten occasions in the autumn, winter, and early spring. The only immature black bird observed closely was recorded in the company of a "normal" adult on March 28, 1953.

We saw black adults four times at rather widely scattered localities on the southern portion of the area in November, 1952, and we believe at least three individuals were present. On March 22, 1953, we saw one which seemed to be paired to a "normal" bird, but we could not relocate it and we think it left the area. In March, 1954, three different black adults were observed, two of which were migrating north at medium elevation. The third again appeared to be one of a pair and acted as though it were nesting, but it could not be found again later. In 1955 one black adult was observed on March 16.

Black Red-tails were never seen on the area in December or January, but they were observed at that time off the study area in southern Green County. Birds in this plumage were never observed in the summer in southern Wisconsin, and there is no evidence that they ever breed there.

THE HORNED OWL POPULATION

Winter population.—In the late fall and winter, owls roosted in the larger and denser stands of timber, but they used small ones if no large woodlots were available. By visiting each woodlot on the area several times throughout the winter we are certain that we located every bird on the area.

Birds were reluctant to leave the cover of their roosting woods and after being flushed several times they doubled back, often quite close to us. Birds of a pair generally roosted in the same woodlot and by early January the shift to the nesting area, if any, had been made. Similarly, Errington (1932*b*) found that all but one of 29 pairs moved into their nesting areas in late fall and Baumgartner (1938) stated that the nesting site is selected several months before the eggs are laid.

Fig. 5. Young Red-tailed Hawks nearly ready to leave the nest. At this age they begin to jump from the nest at the approach of the climber.

Population density.—There were 20 pairs of Horned Owls and one unpaired bird on the study area in 1953 (0.22 pairs per square mile), 19 pairs in 1954 (0.20 pairs per square mile), and 11 pairs and 4 single birds in 1955 (0.12 pairs per square mile). Near Prairie du Sac, Wisconsin, Errington, Hamerstrom, and Hamerstrom (1940) found 0.5 pairs per square mile, but we know of no other accurate census of Horned Owl populations over significant areas. Baumgartner (1939) heard three or four hooting males per square mile near Lawrence, Kansas, and estimated the population at two pairs per square mile. In California, Fitch (1940, 1947), also counting hooting birds, estimated three to four pairs per square mile. In neither of these instances, however, was the hooting count followed by an intensive search for nests so that it is impossible to judge the accuracy of this method of sampling Horned Owl populations.

Breeding.—Since we searched all woodlots and scattered trees on the area carefully, we believe that for the three years of the study we found all the breeding and nonbreeding birds on the area. We began intensive searching for nests in mid-February

when nearly all birds had begun incubating. However, we made no attempt to investigate nests before there were young for fear the eggs would be chilled in the cold winter weather. We calculated the date of egg laying by estimating the age of young at the time of banding, using an accurately dated nest for reference, and adding to that the 33- to 37-day incubation period (Hoffmeister and Setzer, 1947; Elder, 1935).

Most birds laid their eggs between February 5 and 15 but one pair in each of two years laid in the last five days of January. In 1954 one bird did not lay until February 25, the latest laying date for the 48 nests studied.

The birds on our study area used old tree nests of hawks, crows, herons, and squirrels. We found no evidence that owls ever built or remodelled any of these nests and Errington (1932*b*) reports the same for 29 additional Wisconsin nests. Watson (1933) found an old Red-tailed Hawk nest which had been enlarged and newly lined with owl feathers and thought that owls had done the building. Lang (*fide* Baumgartner, 1938), reported a nest at Indian Head, Saskatchewan, Canada, which was built closer to his house than crows had previously chosen, and he was positive that owls had built it entirely. However, in neither instance were owls seen to carry sticks. We have seen owls take over nests freshly repaired by Red-tails and doubt that the Horned Owl builds.

Of the 48 Horned Owl nests we found in the course of the study, 31 were in old Red-tailed Hawk nests, 4 in Cooper Hawk nests, 3 in crow nests, 2 in fox squirrel nests, 1 in a Great Blue Heron (*Ardea herodias*) nest, and 7 in nests of unknown origin. Even if a nest had not been used for several years, we could recognize old Red-tailed Hawk nests by their construction and location. Of 29 nests in southern and central Wisconsin found by Errington (1932*b*), 13 were in Red-tailed Hawk nests, 8 in crow nests, 3 in hollow trees, 2 in unidentified stick nests, 2 in holes in rock faces, and one in a fox squirrel nest. Most Horned Owls in the eastern part of the United States nest in trees (Baumgartner, 1938; Kirkwood, 1925), but in the west, cliff sites are frequently used (Dixon, 1914) and even ground nests are found (Fitch, 1947). In spite of the adaptability of the Horned Owl we feel that on our study area, where there are no cliffs and the trees are cut before they are old enough to have large cavities, the population of Red-tailed Hawks aids the owls greatly in the breeding season by providing many suitable nests.

Thirteen nests were enclosed on all sides by dense woods, 5 were on the edges of woods, 19 were on open, grazed woodlots, and 4 were in very open localities where the few trees were more than 50 feet apart. The locations of nests are shown in figure 3. The nests we measured ranged in height from 25 to 91 feet with an average of 59 (±16.99 feet). The owls sometimes moved as far as one-half mile from their roosting site to find a suitable nest but occasionally a pair left its roosting woods for no obvious reason. One pair left a woods containing eight Great Blue Heron nests and one Red-tailed Hawk nest and used a crow nest only 25 feet from the ground one-third mile away.

Since the nests used by the owls are already at least one year old, they are generally usable for only one year. We found only one nest used two years in succession and by the end of the second year most of it had fallen from the tree. Sometimes, however, nests were repaired and used by Red-tailed Hawks the following year and then were used again by the owls.

The unpaired birds on the area may serve the important function of replacing mated birds which die in the course of the breeding season. This was not observed on the study area, but 30 miles to the north on March 4, 1954, we found an adult male, which had been dead for only a few hours, about 200 feet from a nest. A careful search revealed no owls in the vicinity other than the incubating female. When we revisited the nest on March 9 there were two birds and they successfully raised two young. We do not

know how or where the female acquired her new mate. Such replacements may occur more frequently than our records indicate, as these situations are difficult to detect.

Non-breeding pairs formed a characteristic part of the owl population. Six pairs out of 20 in 1953, 6 pairs out of 19 in 1954, and 1 pair out of 11 in 1955 failed to breed. When a nest could not be located, we searched the area carefully several times to be certain that a hollow tree or ground site had not been overlooked. Failure to breed might be caused by human disturbance, but since several times we observed successful nesting in woodlots that were being selectively lumbered we feel that this is unlikely. Lack of a suitable nest could be advanced as a factor in some instances but on three occasions pairs used nests a second year which were present the year they failed to nest. We think that a likely cause of non-nesting could have been that one of the pair was a yearling incapable of breeding, but we did not collect any birds to test this.

Horned Owls in Wisconsin brood their young constantly for several weeks. In cold weather we could not flush incubating birds by pounding on the tree trunks and we observed an adult brooding one-month-old young on a day when the temperature was 70°F. This brooding tenacity is in marked contrast to the behavior of the Red-tailed Hawk and would seem to be necessary if the species is to nest as early as it does.

It was not possible for us to determine the length of time the young normally remain in the nests as our visits caused many of them to leave prematurely. We closely observed a number of fledglings that had left the nest earlier than normal, and all of them survived. One young bird moved into an old fox squirrel nest where the adults continued to feed it. Since newly fledged birds are so clumsy that they have great difficulty in landing on tree branches, it must be several months before they are able to catch their own prey. The young of the smaller Tawny Owl (*Strix aluco*) are totally dependent upon their parents for three months after leaving the nest (Southern, 1954).

We considered a nest successful if one young bird was raised to the age where it could be expected to leave the nest. Our observations show that most nestling mortality occurred in the first three weeks after hatching. The success of Horned Owl nests for the three years was 1.6, 2.0, and 1.8 young per nest (table 2).

With the exception of one nesting failure in 1954 correlated with logging in the vicinity of the nest, we do not know the causes of nesting failure and cannot explain the differences between the years. Clutch size may vary from year to year, but this is doubtful.

After nests failed we searched the vicinity for adults and always found both parents, so that failure could not have been due to the death of one of the birds. If cold weather were the cause, 1954 should have been the poorest nesting year and not the best, as March of that year was very cold, while the other winters were comparatively mild and snowless. As we were unable to census the populations of the chief prey species (other than by kill records—table 3) on the study area we do not know how likely it is that the young starved. We never found dead young in the nests to examine. Even if prey were plentiful, it might be that a few nights of bad hunting at hatching time would prove fatal to the tiny young. Horned Owls also hunt in the daytime with some success (Fitch, 1947; Vaughan, 1954; Packard, 1954), but prey taken in daylight may be insufficient to offset night failure.

Nestlings vanished from unsuccessful nests and they may have been taken by predators. We feel that the Red-tailed Hawk is the most likely predator species. Fitch (1940) thought that the Red-tail was the most likely predator of one California nest. Other California failures were due to weather, raccoons, and unsanitary conditions created by uneaten prey (Fitch, 1940, 1947).

In the course of the study we banded over 70 young owls, but we have only one recovery, a nestling banded on March 27, 1954, and recovered on October 9, 1954, one-half mile south of the banding location. Errington (1932*b*) obtained three recoveries

from 13 birds banded, all at points 13 to 20 miles from the banding location. We found one adult which had died of a virus infection (Animal Disease Diagnostic Laboratory, University of Wisconsin). The symptoms were similar to those of a dead bird found by Errington (1932*a*), but unfortunately specific determination of the virus was not possible. Golden Eagles sometimes kill owls in the western states (Dixon, 1937; Carnie, 1954) but we know of no important predator of adult owls in Wisconsin.

Fig. 6. Young Horned Owls in nest with remains of an adult cottontail, their principal food on the study area.

Food.—Our studies of the food of the Horned Owl have been limited to the late winter and spring. Pellets collected near the nests contained the following food items: 100 *Peromyscus,* 34 *Microtus,* 17 cottontails, 5 *Mus musculus,* 4 *Blarina brevicauda,* 4 *Rattus norvegicus,* 3 woodchucks (*Marmota monax*), 2 crayfish (*Cambarus*), 1 thirteen-lined ground squirrel, 1 Screech Owl, 1 meadowlark (*Sturnella* sp.), and 1 unidentified passerine.

In the nests we found the remains of 43 cottontails, 30 Ring-necked Pheasants, 7 Yellow-shafted Flickers, 5 American Crows, 3 Rock Doves, 4 meadowlarks, 4 Grackles (*Quiscalus quiscula*), 1 Robin (*Turdus migratorius*), 1 *Peromyscus* sp., 1 *Microtus* sp., 1 chicken, and one Starling.

Cottontails seem to be the chief food of the Horned Owl over much of its range (fig. 6). In California, cottontails formed 61 per cent by weight of the food of the owls (Fitch, 1947), and in parts of the north-central states the percentage is even higher (Errington, Hamerstrom, and Hamerstrom, 1940). The owls on our study area ate far more pheasants than in any other region where they have been studied.

DISCUSSION

Populations.—In this three-year study, the population density of Red-tails varied from 0.41 to 0.29 pairs per square mile. That of the Horned Owls ranged from 0.21 to

0.14 pairs per square mile. However, if the prairie areas, where the owls do not nest, are subtracted from the total area, we have an owl population density of 0.38 to 0.22 pairs per square mile for the three years. There is no evidence which would indicate that human interference other than habitat alteration kept the numbers down.

Thirty-one of the 48 owl nests were built by Red-tails, and as the hawks often re-use their nests, these two species sometimes compete for nests. We saw hawks working at a nest in early February, 1952, but owls were using it in March. On April 11, 1955, we found a Red-tail incubating on a nest which the owls had been using in February. In the course of the study, both species simultaneously nested in the same woods 14 times. Flushed owls were never attacked by adult hawks but we did see immature hawks diving at owls flying in the open on several occasions. On February 21, 1954, we saw an adult Red-tail dive several times at an incubating owl.

In 1954 owl nesting success was best (1.9 young per nesting pair), but in this year the Red-tail success (1.1 young per nesting pair) was the poorest of the three years (table 2). A combination of competition for food and direct interference may be responsible, but more evidence is needed. For unknown reasons the numbers of both species decreased between breeding seasons of 1954 and 1955.

Food relationships.—When considering the food of the Red-tailed Hawk and the Horned Owl the following limitations of our data must be kept in mind: (a) Pellets cannot be used to give a fair quantitative appraisal of the food of the Red-tail. (b) Data were obtained only in the breeding season. (c) The data for the Red-tail were obtained a month later than those for the Horned Owl. (d) Only a few of the most abundant prey species can be discussed profitably because of the small number of data.

It is interesting that pheasants and cottontails were the principal food of both the Horned Owl and Red-tailed Hawk in Green County throughout these breeding seasons. We do not know how similar the food is in the remainder of the year, but our data from the breeding season suggest that these two species have converged in their food selection until they are more similar than various groups of closely related species of birds which have been studied (Lack, 1944, 1945, 1946). This suggests that it would be worthwhile to study the interactions between diurnal and nocturnal predators hunting the same prey species in the same area.

Timing of the breeding season.—With the exception of an occasional crossbill, Horned Owls are the first birds to breed in central and northeastern North America, egg-laying beginning at the coldest time of year. This may be because their food is most readily obtainable early in the spring or because the long post-fledgling period must be completed before cold weather returns.

The critical period for food would seem to be the first few weeks after hatching when one adult must hunt for its brooding mate and young in addition to itself. If breeding began later, it would be possible for both adults to hunt without danger of the young being chilled. It is therefore surprising to find that the numbers of both pheasants and cottontails are lowest at this time when we would expect the greatest strain upon the hunting adult. Before the middle of April, young cottontails are hidden in their nests where apparently they are not vulnerable to predation by owls. The breeding season of pheasants does not begin until May and June, long after the young owls have left the nest.

In spite of their small numbers, however, the prey species may be more vulnerable in early spring when the snow disappears and the flattened vegetation offers the least protection to ground-dwelling animals of any time of the year. Southern (1954) states that woodland owls must breed early in the year, in spite of the cold weather, to enable them to feed their young before the growth of vegetation on the forest floor effectively

conceals their favorite prey, whereas field owls are able to hunt with greater ease throughout the summer so that breeding can be much later and more prolonged. It is difficult to classify the Horned Owl into either of these two categories. In most of eastern North America the species is predominately a forest inhabitant but in the mid-west and far west, it may hunt almost exclusively in open country. In southern Wisconsin it must hunt regularly in both places.

On the other hand, the breeding season may be early because postfledgling survival is better in early broods which learn to hunt and disperse in the early autumn when hunting is easy. Until we have more information on the activities of the young in that crucial period when they are becoming independent of their parents, it is impossible to say which of the two reasons is the important one, or if the breeding season is a compromise between the two.

Table 4

The Food of Four Important Rodent Predators in California*

Prey species	Horned Owl	Coyote	Red-tailed Hawk	Rattlesnake
Cottontail	61.1	45.4	24.2	15.2
Woodrat	17.9	4.9	1.1	1.7
Kangaroo Rat	4.5	3.3	0.2	5.9
Pocket Gopher	4.3	3.5	7.4	2.4
Gopher Snake	3.7	6.0	9.0	.....
Ground Squirrel	2.4	31.2	49.5	70.5
Others	6.1	5.7	8.6	4.2

* Data from Fitch (1947); per cent composition by weight.

The study of animal populations.—Our studies of the Red-tailed Hawk and Horned Owl show that these two species occupy and forage over the same areas, and that pheasants and cottontails are the most important foods for both of them in the breeding season in southern Wisconsin. The studies of Fitch (1947) in California give further evidence of the similarity of the food selected by unrelated species of predators inhabiting the same area (table 4). Pitelka, Tomich, and Treichel (1955) stated that in northern Alaska lemmings formed the chief food for a variety of unrelated predators, namely, Pomarine Jaeger (*Stercorarius pomarinus*), Snowy Owl (*Nyctea scandiaca*), Short-eared Owl (*Asio flammeus*), arctic fox (*Alopex lagopus*), and least weasel (*Mustela rixosa*). Many other examples of this could be cited.

Lack (1944, 1945, 1946) studied many closely related species of birds and found that they all differed strikingly in food and habitat requirements. The same has been found for snakes (Carpenter, 1952) and insects (Diver, 1940). Elton (1946) and Moreau (1948), examined the species composition of a number of arbitrarily defined animal communities and found fewer closely related species occurring together than would be expected if species were randomly distributed. That closely related species, in these cases, differ in habitat and food requirements is interpreted by these authors as indicating that no competition occurs between them today. They have therefore assumed that it must have occurred in the past when the two species came together after their differentiation in geographical isolation from one another. Where their ranges overlapped they "competed" and drove each other into different niches. It is also assumed that the species evolved differences in behavior and structure in response to that niche in which they were successful. But as Andrewartha and Birch (1954:463) have stated, if we assume that "related species have differentiated in geographic isolation, the chances are that they would also have developed different habits and preferences, so

that when they were later brought into the same territory, they would select different sorts of places in which to live. It is not obligatory to suppose that these preferences were developed as a result of 'competition'."

We feel that the study of closely related species that has dominated the attention of students of population ecology in the past two decades may not lead to so complete an understanding of certain dynamics in natural communities as has been expected. Since closely related species seldom occupy the same habitat, the worker is forced to postulate what he thinks must have happened in the past, and to pose hypotheses which can be neither proved nor disproved. We believe that it is equally desirable to study *unrelated* species which are coming into frequent contact with one another. Then it is not necessary to postulate what we think must have happened in the past but we can directly study the present-day levels of interaction among the species of a community. As Elton (1946) pointed out, little is known about the relationships among species drawing on a common resource, the most frequent of all species interactions. That this type of study has been neglected testifies to the unfortunate grip of the "competition in the past" theory on ecological thought and stresses the need for a widening of approach.

SUMMARY

The populations of the Red-tailed Hawk and Horned Owl on 95 square miles of farm land in Green County, Wisconsin, were studied for three years. In this time we believe all resident birds of both species were located and all nests were found.

Red-tailed Hawks hunted singly or in groups throughout the winter but were paired on territories by the end of February. There were 27 nests in 1953, 33 in 1954, and 27 in 1955. Nests were built as early as the end of January but eggs were never laid before March. Nesting success was 1.8 young per nest in 1953, 1.1 young per nest in 1954, and 1.4 young per nest in 1955. The causes of nest failure could not be determined.

Horned Owls did not build their own nests but used old nests of hawks (35), crows (3), herons (1), and squirrels (2). There were 13 nests in 1953, 17 in 1954, and 11 in 1955. All pairs on our area moved into their nesting area by early January and the first eggs were laid by the end of the month. Nesting success was 1.1 young per nest in 1953, 1.9 young per nest in 1954, and 1.3 young per nest in 1955. Thirty-one of the 48 Horned Owl nests we found were in old Red-tailed Hawk nests, and we feel that Red-tails greatly aid the owls by providing a large number of excellent nests.

Pheasants and cottontails were the principal foods of both the Red-tailed Hawks and Horned Owls in the breeding season, and the two predator species may compete for food. They sometimes competed for nests. They may occasionally prey directly upon each other's young.

The authors believe that unrelated species offer the best opportunity to study the interactions of animal populations as they occur together in most habitats. The study of closely related species inevitably leads to postulations of what the observer feels must have happened in the past to produce present-day differences.

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Department of Zoology, University of Wisconsin, December 17, 1955.

FROM FIELD AND STUDY

Clark Nutcrackers Preying on Ground Squirrels and Chipmunks.—On April 19, 1935, a nest of the Clark Nutcracker (*Nucifraga columbiana*) was found in the lower branches of a juniper tree on a warm south slope near the shore line of Gull Lake, Mono County, California. After waiting two and a half hours the parent nutcrackers arrived and proceeded to brood the three shivering youngsters in the nest. Following a few minutes of brooding, a parent bird began regurgitating square-shaped chunks of fresh meat and fed each young until it refused any further food. We were puzzled as to where the parent bird could have obtained this fresh meat.

As we left the nest we heard a commotion on a slope beyond a slight rise in the ground. Hurrying there to see what was going on, we found an adult nutcracker battling with a Belding ground squirrel (*Citellus beldingi*). The nutcracker soon won the battle. We stood within 25 feet of the bird and watched it skin back the hide from the carcass of the squirrel and proceed to tear off the fresh meat in square chunks. In a very short time the nutcracker had finished the job of tearing off the meat from the squirrel. It then flew away in the direction of the nest we had found.

Our field notes show that on this same trip we saw two instances of the nutcrackers attacking chipmunks. In one case the nutcracker killed the chipmunk and ate it. In the other case the chipmunk escaped. This is the only season in which we have ever observed such action on the part of the nutcrackers in the twenty-six years we have spent in the area. In 1935 there was an unusually large number of nesting nutcrackers in this part of Mono County.—James B. Dixon, *Escondido, California, May 6, 1956.*

A Collection of Panamanian Nests and Eggs.—A small collection of Panamanian nests and eggs acquired by the Chicago Natural History Museum several years ago contains a number of specimens that are noteworthy, either by virtue of their uniqueness or because there is need for further information relating to the breeding habits of the species represented. The specimens described here were collected approximately 5400 feet above sea level on the slopes of Volcán de Chiriquí, a classic collecting locality, by Señor T. B. Mönniche, proprietor of Finca Lerida, Boquete. A report on some 1600 bird skins collected in the same region by Señor Mönniche approaches completion and will be published later by the Chicago museum.

Oreopeleia linearis chiriquensis. White-faced Quail-Dove. A nest collected on August 24, 1950, is constructed of twigs from a coffee tree and coarse roots loosely arranged in the form of a very crude platform lined medially with somewhat finer roots; the diameter is 14 inches. This nest, located eight feet above the ground on a bent primary branch of a coffee tree, was partly supported by a mass of smaller branches. The nest material is surprisingly coarse. One twig is 30 inches long and has a maximum diameter of ¼ inch. The two eggs are deep creamy white, with a slight gloss, and measure 33.7×24.9 and 32.4×25.1 mm. Incubation was advanced. It is noteworthy that two Costa Rican nests mentioned by Carriker (Annals Carnegie Museum, 6, 1910:408) contained fresh eggs as late as September 16.

Phaethornis guy coruscus. Green Hermit. A nest collected on May 9, 1932, is cone-shaped and slightly flattened on one side where attached to a palm leaf. It is made almost wholly of very fine plant fibres and grass intermixed with moss near the rim of the cup. The inside of the cup is lined with feathery seeds of a vine. Dimensions of the nest are 3×8 inches, the cup being 1¼ inches in diameter and 1½ inches deep. The nest was firmly attached by means of a thin network of exceedingly fine fibres to the underside of the tip of a palm leaf which served as a roof to the cup. The two dull white eggs, accidentally destroyed, measured 17×11 and 18×11 mm. Incubation was advanced (Mönniche notes).

According to Mönniche, a large number of Chiriqui hummingbirds adopt a nesting site similar to the one described here and Worth (Auk, 59, 1942:367) has previously reported a Green Hermit nest of this type.

Selasphorus scintilla. Scintillant Hummingbird. Three nests with incubated eggs were collected on November 4 and December 12, 1932. These nests are similar in general appearance—compact, cup-shaped structures of moss, more or less covered with lichens; but their respective bowls are lined with

white cottony plant-fibres, brown scales from a fern-stem, and feathers from an undetermined passerine bird. Average dimensions of the nests are 1½×1¼ inches. The cups measure approximately ⅞×⅝ inches. Each nest contained two dull white eggs. Measurements of two clutches: 12×8 and 11.5×8; 11.5×8 and 11×8 mm.

Trogon aurantiiventris aurantiiventris. Orange-bellied Trogon. A nest containing one incubated egg found on July 2, 1932, apparently is the first of record. The nest cavity, six feet above the ground in a large tree, was caused by the rotting of a branch. The single immaculate white egg is slightly glossy and measures 26.9×22.5 mm. It was deposited on the "sawdust" and rotten wood of the cavity's floor, which bore no evidence of introduced nesting materials.

Empidonax flavescens flavescens. Yellowish Flycatcher. Two nests with incubated eggs were collected on April 13 and May 26, 1932. Both nests are made of firmly packed moss and have rounded cups lined with hair-like roots and fibres. Outside dimensions of one nest are 3½×4 inches. Its cup is 1¾ inches in diameter and 1½ inches deep. Both nests were found in rock crevasses adjacent to creeks, one foot and four feet, respectively, above the water. One nest contained three eggs, the other only two. The eggs are dull creamy white, with chestnut-rufous spots and blotches concentrated chiefly at the larger end. Measurements of one clutch: 18×14.5, 18×14.5, 18.5×14 mm.

Elaenia chiriquensis chiriquensis. Lesser Elaenia. A nest found five feet above the ground in a peach tree on May 6, 1933, seems to be the first of record for this species. This nest is made of fine rootlets and has several pieces of string woven into its base. White chicken feathers line the cup. Dimensions: 3½×2 inches; the shallow cup 1¾×1 inch. The two partly incubated eggs are dull white, with a scanty halo of small chestnut spots around the larger end. Only fragments of these eggs were preserved, but the collector's field notes indicate that one egg had a transverse diameter of 14 mm.

Elaenia obscura frantzii. Dusky Elaenia. Three nests with eggs were found near the ground in coffee trees on April 6 and May 26, 1932. Each of the nests is made of fine rootlets and has an outer covering of moss. The cups of two are lined with horsehairs and all contain feathers, among which can be recognized those of a chicken and of a wild pigeon. Average dimensions of the nests are 3½×2 inches, the cups being approximately 2½ inches in diameter and ¾ inches deep. Each nest contained two dull white eggs marked, chiefly on the larger end, with a few reddish-brown spots and dots. Measurements of three eggs: 21.3×16.5, 18.5×14.9, 18.8×15 mm.

Thryothorus modestus modestus. Plain Wren. A nest found in a low bush on May 10, 1932, contained two partly incubated eggs. They are dull white, unmarked, and measure 21.5×14.3 and 22.3×14.2 mm. The retort-shaped nest is eight inches high and has a maximum diameter of five inches. It is loosely woven of dry grass, this being finest in the lining. The nest cup is lined with chicken feathers.

Turdus assimilis cnephosus. White-throated Robin. A nest collected on April 28, 1932, contained three partly incubated eggs. These are so heavily speckled and blotched with dull reddish-brown as largely to obscure the pale greenish-white ground color. Measurements: 31.3×20.6, 30.4×20.6, 31×21 mm. The nest, consisting of little more than a shallow cup loosely constructed of coarse twigs, was located 1½ feet above the ground in a large rotten stump. The cup is 3 inches in diameter and 1½ inches deep.

Turdus grayi casius. Clay-colored Robin. Three nests containing incubated eggs were collected on May 28, 1932, and May 15, 1933. The nests are compact structures of moss intermixed with earth and are lined with coarse rootlets. A turkey feather is imbedded in one of the cups. Two of the nests were located seven feet above the ground in coffee trees; the third was twenty feet above the ground in an orange tree. The clutches of eggs number 3, 3 and 2, respectively. All have a pale greenish-white ground color, but there is much variation in the markings. These consist of reddish-brown or chestnut spots or specks concentrated chiefly at the larger end where sometimes intermixed with lavender. Several of the eggs are virtually interchangeable with those of the preceding form. Measurements of seven eggs: 28.6×20.2, 28.4×19.4, 27.9×19, 27.8×19.6, 27×18.9, 26.2×19.3, 25.7×19.2 mm.

Myadestes ralloides melanops. Black-faced Solitaire. I find no reference to the nest and eggs of this thrush although it is a notable songster and quite abundant in humid mountain forests both in Costa Rica and in western Panamá. A nest collected on March 30, 1932, was located in the crevice of a rock about three feet above a road. It is made almost wholly of soft moss and has a smooth lining of black hair-like rootlets. Dimensions: 6×5×2½ inches, the cup 3½×2½×½ inches. The two eggs, partly incubated, measure 24×16.7 and 22.8×16.9 mm. They are pinkish-white, minutely speckled

with dull chestnut except toward the larger end where they are increasingly spotted and blotched with the same.

Catharus aurantiirostris russatus. Orange-billed Nightingale-Thrush. A nest and two partly incubated eggs collected on May 13, 1932, apparently are the first of record. The nest was located eight feet above the ground in a small tree. It is a compact structure of moss, much like that of *Myadestes ralloides melanops* described above, but it has a few bits of dried leaves and plant stalks woven into its base and side. The cup is neatly lined with black, hair-like rootlets. The outside dimensions are 5½×4½×3 inches. The cup 2½×1¾ inches. A single egg of the pair was preserved. It is pale greenish-white, thickly and almost uniformly speckled with light reddish brown; it measures 23.4×17.3 mm. The collector's field notes state that the second egg was similar in color and measured 23×18 mm.

Tanagra musica elegantissima. Blue-hooded Euphonia. The eggs of this tanager have been described on several occasions but I find no reference to its nest. An example collected on May 13, 1932, was located fifteen feet above the ground in the crown of a tree and is a masterpiece of camouflage. It is constructed of green moss and surmounts a large shapeless mass of the same material. The nest measures 4×3½×5 inches and has a pouch-shaped cup, three inches in depth but only one inch in diameter at the rim. Pale, hair-like rootlets line the cup. The two creamy white eggs are spheroidal in shape and thickly dotted, especially at the larger end, with small sharply defined spots of very dark purplish-brown and dull chestnut. Incubation was begun. Measurements: 17.6×13.8 and 18×14 mm.

Piranga bidentata sanguinolenta. Crimson-collared Tanager. Two nests collected on March 19 and May 10, 1932, are loosely constructed of dry twigs, small roots and tendrils. Fine grass stems line both cups and a few horse hairs are woven into the sides of one. Outside dimensions of these nests are 5×2½ inches, the cups 3×1½ inches. One of the nests was located three feet above the ground in a tangle of bushes and vines; the other was found seven feet above the ground in a coffee tree. The eggs, in clutches of three and two, respectively, were partly incubated. They are pale blue and rather lightly speckled, chiefly toward the larger end, with reddish-brown intermixed with dark lavender. Measurements of one clutch: 23.1×17.8, 23.4×18, 22.5×17.2 mm.

Atlapetes gutturalis brunnescens. Yellow-throated Brush-Finch. A nest collected on April 11, 1932, is made entirely of grass and straw-like materials, finest in the lining, and measures 5×4×2½ inches. Its cup is shallow and ill-defined. This nest, unlike others of the species that have been described, was built on the ground. The two immaculate white eggs are slightly glossy and were faintly tinged with blue when found. Measurements: 23.5×16.3 and 23×16.5 mm.

Zonotrichia capensis costaricensis. Rufous-collared Sparrow. A nest and two incubated eggs collected on February 23, 1933, are especially noteworthy in that previous breeding records of the species in Central America have been limited to the period from April to September, inclusive. This nest, found on the ground at the base of a precipice, is a loosely made structure of coarse straw, grass and leaves. The cup is lined with very fine grass stems and skunk hair. Outside dimensions of the nest are 4½×5×3 inches, the cup 2½×1¼ inches. The two eggs are bluish-white, generously and almost evenly speckled with lilac and reddish-brown. Measurements: 20×16 and 20.5×16 mm.—EMMET R. BLAKE, *Chicago Natural History Museum, Chicago, Illinois, March 29, 1956.*

Land Birds at Sea Off Southern California.—A number of occurrences of land birds at sea off southern California were recorded in May of 1951 (Wisner, Condor, 54, 1952:62–63). On September 25, 1953, an entirely different group of land birds was observed on board the research vessel E. W. Scripps at latitude 32° 34.6′N., longitude 117° 21.5′W. The nearest points of land were Point Loma, 8 miles northeast and the Coronados Islands, 8.5 miles to the south. The ship was surrounded by a heavy fog, and visibility aboard was reduced to about one-half mile. The foggy condition had prevailed for several days prior to these observations. The sea was calm and the air temperature about 72°F. The ship was at anchor during the night at this location prior to the following recordings.

The observations were made between 7:30 a.m. and 9:30 a.m. The first bird, a Long-billed Marsh Wren (*Telmatodytes palustris*, probably *plesius*; specimen damaged in capture) was found feeding on a moth that had become lodged in some electrical cable on deck. The wren's actions indicated that it had already become adapted to shipboard life, as it flitted about with complete composure. At the same time a Brewer Sparrow (*Spizella breweri*) and a Western Tanager (*Piranga ludoviciana*) were observed to be aboard. The sparrow seemed to be shy and retired to a secluded spot when disturbed.

The tanager flitted into the air from time to time to capture insects. Its condition, however, was apparently weakened by the sojourn at sea, since it was easily captured by hand. The wren and the sparrow were less easily taken. While the writer was in pursuit of them, a Warbling Vireo (*Vireo gilvus swainsonii*) and a Ruby-crowned Kinglet (*Regulus calendula cineraceus*) appeared. Fortunately, the vireo soon flew by at close range and was captured by hand while in flight. The kinglet was taken in a similar manner.

On top of the deck house, a Mourning Dove (*Zenaidura macroura*) had alighted. When frightened, it circled the ship repeatedly but returned unnoticed. The dove lacked its upper tail coverts and was easily recognized as the same bird when rediscovered. It did not return from a second flight.

The specimens of the tanager, vireo, kinglet, and wren are deposited at the San Diego Natural History Museum, where the identifications were verified by Mr. Laurence M. Huey.—ANDREAS B. RECHNITZER, *Scripps Institution of Oceanography, La Jolla, California, April 10, 1956.*

Footprint of a Bird from the Miocene of Louisiana.—Through Dr. Julia Gardner of the United States Geological Survey there came to me for study a slab of sandstone of Miocene age from near Bentley, Grant Parish, Louisiana, that shows two fossil footprints in bold relief on the surface of the rock. The specimen, which is the property of the finder, Mr. B. N. Eubanks of Dry Prong, Louisiana, was forwarded by him for identification to the Louisiana Geological Survey at Baton Rouge and was sent to Washington for study by Dr. Grover E. Murray, Chairman of the Department of Geology at Louisiana State University. According to information received from Dr. Murray, the tracks come from the Catahoula Formation, which is attributed to the Lower Miocene.

While the two casts are generally similar (see fig. 1) they differ slightly in size. Apparently, they come from two sets of tracks that trend in the same general direction but tend to cross, as the impressions are at a slight angle with one another. Seemingly, the lower footprint is from a left foot and the upper one from the right side, as indicated by the relative lengths of the two lateral toes. The upper track is more heavily formed and is slightly larger. The impressions show three anterior toes clearly, while in the upper one at the rear on the left there is a faint, rounded depression that may be an indication of a hind toe. Separate phalanges are not indicated except for the narrowed points on certain of the toe-prints that represent short claws. Rather broad fusion at the bases of the toes in both tracks indicates the presence of small webs. Since only the two units in two apparently separate trackways are present, there is no indication of the length of the stride. The approximate length of the longest track, including a very faint indication of claw on the distal end of the middle toe, is 97 mm. The dimension across the spread of the lateral toes is 79 mm. The smaller track measures 86 mm. in length and 71 mm. in breadth.

The preservation of tracks in fossil form is intriguing to the mind and attractive to the eye, as well as an interesting puzzle, particularly to persons of hunter training who in their outdoor excursions examine the ground for footprints and other sign as they pass along. In the present instance there seems to be no reasonable doubt that the animal concerned was a bird and not a reptile. The casts are distinctly avian in appearance, and the Miocene locality makes their identification as avian reasonable.

The species apparently was one of considerable weight to judge from the evident depth of the impression made by the foot, and one with strong and heavy, but relatively short, toes armed with rather small claws. After some consideration of foot-form in such large living birds as tinamous, screamers, vultures, fowls, cranes, cariamas and thick-knees, and of various fossil species where the foot is known, it is thought that the proportions of the toes relative to one another, the amount of apparent basal webbing, the heavy form, and the spread of the track suggest a condor-like species. The spread angle of the toes in relation to one another especially agrees with this group. The toes appear heavier and those at either side shorter in relation to the central one than in the cranes, another group that offers some resemblance, and the toes spread too widely for the fowl-like species. The size is that of a medium-sized vulture and the general resemblance of the impressions to the foot of such a bird is striking. Turkey Vulture and Black Vulture tracks usually show an impression of a hind toe, which is less evident in the larger kinds, as is well shown by Olaus Murie in his Field Guide to Animal Tracks (1955:329, fig. 175*a*) in an impression of the track of the California Condor. The fossil imprint is somewhat smaller than the foot of the King Vulture (*Sarcoramphus papa*).

While footprint specimens have had scientific names given to them, particularly where found in

Fig. 1. Fossil footprints from Lower Miocene deposits in central Louisiana.

series in older geologic strata, this does not seem warranted in the present instance since there is no possibility of positive allocation in our system of classification. We have to express thanks, however, to Mr. Eubanks for bringing to attention a highly interesting specimen that appears to be the first representation of any form of bird from the Tertiary of Louisiana.—ALEXANDER WETMORE, *Smithsonian Institution, Washington, D.C., November 15, 1955.*

European Widgeon and Glaucous Gull in Utah.—On October 19, 1955, a duck hunter, hunting on the open area of the Bear River Migratory Bird Refuge, shot a European Widgeon (*Mareca penelope*). This was a male bird in full fall plumage. As this is the first and only record of a European Widgeon in this intermountain area so far as we know, the specimen was added to the Refuge collection of rare and unusual birds for the area.

On March 16, 1955, a Glaucous Gull (*Larus hyperboreus*) was collected at the Refuge. This is the first record of this bird on the Refuge and so far as we know the second report of the bird in the state of Utah. The bird was first observed feeding with several California Gulls on dead fish in unit 3 of the Refuge. The bird was collected and the skin has been placed in the Refuge collection.—VANEZ T. WILSON and LEO T. YOUNG, *United States Fish and Wildlife Service, Brigham City, Utah, May 10, 1956.*

NOTES AND NEWS

At the invitation of the University of California at Los Angeles, the Los Angeles County Museum, and the Los Angeles Audubon Society, the Cooper Ornithological Society will hold its annual meeting in the Los Angeles area on April 26, 27, and 28, 1957.

The editors regret to report the death of Mrs. Winifred S. Sabine whose article on flocking in juncos appears in this issue of The Condor.

The Brewster Award of the American Ornithologists' Union for 1956 was made to George H. Lowery, Jr., in recognition of his research on nocturnal migrations of birds. The new officers of the Union recently elected are: Ludlow Griscom, President; Ernst Mayr, First Vice-president; George H. Lowery, Jr., Second Vice-president. The Secretary, Harold Mayfield, the Treasurer, Charles G. Sibley, and the Editor of The Auk, Robert W. Storer, were re-elected. New Council Members are: Maurice G. Brooks, Donald S. Farner, Thomas R. Howell, and Ralph S. Palmer. Dr. Palmer also was elected a Fellow. New Elective Members are: David A. Munro, William H. Partridge, and F. W. Preston.

COOPER SOCIETY MEETINGS

ANNUAL BUSINESS MEETING OF 1956

The first session of the annual meeting of the members of the Cooper Ornithological Society (a corporation) was called to order by President J. R. Pemberton in 224 Guggenheim Hall, University of Washington, Seattle, Washington, at 10:25 a.m., Friday, June 15, 1956.

The minutes of the meeting of 1955 were read and approved. The following committees were appointed: *Proxies,* John Davis, Howard L. Cogswell, Thomas R. Howell; Nominations, Junea W. Kelly, Garrett Eddy, Donald D. McLean. The meeting was adjourned until June 16.

The second session of the annual meeting was called to order at 9:30 a.m., Saturday, June 16, 1956.

John Davis, reporting for the Committee to Examine Proxies, declared 34 members present and proxies for 768, of a total membership of 1324. A quorum was therefore present.

Junea W. Kelly, reporting for the Committee on Nominations, presented the following names for nomination to the Board of Directors: John Davis, C. V. Duff, Ed N. Harrison, Thomas R. Howell, Alden H. Miller, J. R. Pemberton, Frank A. Pitelka, W. J. Sheffler, Jack C. von Bloeker, Jr.

Mr. Pemberton called for further nominations from the floor. There being none, Donald McLean moved that the nominations be closed and that the Secretary cast a unanimous ballot in favor of the election of the entire slate of the nominated directors. The motion was seconded by Garrett Eddy and unanimously passed.

Mr. C. V. Duff, business manager, presented a report on the financial condition of the Society. Investment of funds under the supervision of the Investment Committee has resulted in a significant increase in the Society's funds. The Endowment Fund now totals $93,740.72. The final disposition of the estate of Dr. Harry R. Painton, in which the Society will share, should be made in 1956.

President Pemberton presented a resolution expressing the thanks of the Society to the University of Washington, the Pacific Northwest Bird and Mammal Society, and the members of the Local Committee for the excellent arrangements made for the 1956 meeting. The resolution was adopted unanimously.

President Pemberton presented a resolution that the Cooper Ornithological Society go on record as deploring and condemning the use of the poison 1080 in pest control. Frank Richardson moved that the resolution be adopted. The motion was seconded by Howard Cogswell and unanimously passed.

There being no further business, the meeting adjourned at 10:00 a.m.—JOHN DAVIS, *Secretary*

COOPER ORNITHOLOGICAL SOCIETY, INC.
STATEMENT OF CASH RECEIPTS AND DISBURSEMENTS
FOR THE YEAR ENDING DECEMBER 31, 1955

CASH IN BANK, December 31, 1954			$9,292.48
ADD: CASH RECEIPTS			
General Publication Fund			
Membership dues, regular and sustaining	$5,015.63		
Subscriptions for The Condor	857.35		
Condor sales	430.93		
Phonograph record sales (7 records sold)	53.42		
Dividends and interest received on endowment funds invested (Note A)	2,751.31		
Contributions received for the publication of The Condor	1,090.00		
Other cash receipts	13.50	$10,212.14	
Avifauna Fund			
Avifauna sales (net, Note B)	$ 897.70		
Sales tax collected on Avifauna sales	5.94		
Postage collected on Avifauna sales	13.13	916.77	
Endowment Fund			
Life memberships and installment payments received on life memberships	$ 650.00		
Contributions	1,121.57		
Bond redemption	100.00		
Sale of corporate stocks	4,094.30	$5,965.87	$17,094.78
			$26,387.26
DEDUCT: CASH DISBURSEMENTS			
General Publication Fund			
Publication costs of The Condor			
Printing	$7,595.16		
Engraving	1,237.22		
Purchase of back issues	1.00	8,833.38	
Cost of phonograph records		4.79	
Administrative expenses			
Northern Division	49.97		
Southern Division	84.06		
Annual Meeting	157.87		
Accounting	150.00		
Business manager	263.78		
Treasurer and secretary	220.40		
Editor	15.00	941.08	
Avifauna Fund			
Sales tax	12.60		
Other disbursements	20.69	33.29	
Endowment Fund			
Purchase of corporate stocks	7,591.41	7,591.41	$17,403.95
CASK IN BANK, December 31, 1955			$ 8,983.31

CASH IN BANK ALLOCATED TO FUNDS AS FOLLOWS:	December 31, 1954	December 31, 1955
General Publication Fund	$8,205.19	$ 6,851.74
Grayson Fund	213.66	.....
Avifauna Fund	873.63	1,757.11
Endowment Fund (to be invested)	.....	374.46
	$9,292.48	$ 8,983.31

NOTE A: At December 31, 1955, the business manager had in his custody endowment funds invested in corporate stocks which cost $32,201.40 and had a market value of $78,390.75. The broker reports the credit balance of the Society as of December 31, 1955, totalled $13,578.40. The market value of securities plus the credit with broker totalled $91,969.15. This endowment fund includes the contributions received in the names of Florence M. Bailey, Louis B. Bishop, Albert E. Colburn, Joseph Grinnell, Harry R. Painton, and Isabel A. Thomson.

NOTE B: At December 31, 1955, the Society had a stock of Avifaunas for which the total of the quoted list prices was $30,956.50.

C. V. DUFF, *Business Manager.*

***For Sale, Exchange, and Want Column*—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.**

WANTED—Bent, Life Histories of N. Amer. Flycatchers, Larks, Swallows, and Their Allies; U. S. Nat. Mus. Bull. 179.—KEN LEGG, *Prairie Creek State Park, Orick, Calif.*

WANTED—Copies of the Everglades Natural History Association magazine.—STANFORD C. TICE, *78 Manhattan Ave., New York 25, N.Y.*

FOR SALE—Volumes of The Auk from 1924 to 1940; also certain vols. of Journal of Mammalogy, Condor, and Wilson Bulletin before 1940. Write for specific volumes and prices.—DAVID E. DAVIS, *615 N. Wolfe St., Baltimore 5, Md.*

FOR SALE—Eimer, Organic Evolution, $7.50; Fuertes, Abyssinian Birds and Mammals, portfolio 32 col. pls., $32.00; Goldman, Biol. Investigations in Mexico, $3.50; Shelford, Animal Communities in Temperate America, $8.00.—H. H. T. JACKSON, *National Museum, Washington 25, D.C.*

FREE CHRISTMAS OFFER TO BIRDERS!—With each new binocular sold before Christmas this year, we offer a rainguard and three chrome initials—all gifts on trial until 10 days after Christmas. Free service: All glasses we sell are checked in our shop and guaranteed adjusted to U.S. Government specifications. Six models we adapt specially for ornithologists. Free to C. O. S. members: Our articles reprinted from Audubon Magazine—regularly 10¢. Also, binocular repairs that often make a glass better than new; cleaning and aligning done in 5 days.—WRITE: THE REICHERTS, *Mirakel Repair Co., 14 W. First St., Mount Vernon 15, N.Y.*

FOR SALE—Stephens, California Mammals, $2.50; Loomis, Review of Albatrosses, Petrels and Diving Petrels, $2.50; Cooper, Ornithology of California (newly bound), $5.00; Barrows, Michigan Bird-life, $2.50; Bailey, Birds of Virginia, $2.50; Merriam, Mammals of the Adirondacks, $2.50; Cory, Birds of the West Indies, $3.00; Sudworth, Forest Trees of the Pacific Slope, $1.75; Barrows, The English Sparrow in North America, $1.50; Ridgway, The Hummingbirds, $2.00; postage extra on all orders.—LAURENCE M. HUEY, *Natural History Museum, Balboa Park, San Diego 1, Calif.*

FOR SALE—The "Tiny Tucker" Hummingbird Feeder, complete with instructions for use, $1.15 (incl. postage). Profits from sales help maintain this wildlife sanctuary.—TUCKER BIRD SANCTUARY, *Box 53, Star Route, Modjeska Canyon, Orange, Calif.*

FOR SALE—Check-list of the Birds of Texas. Brief distributional notes with common names of species and technical names of all species and subspecies recorded within the state. Recently published, paper cover, $1.75, postpaid.—COL. L. R. WOLFE, *Route 1, Kerrville, Texas.*

FOR SALE—Japanese "mist" nets, suitable for capturing birds or bats alive and unharmed for banding purposes. Send for price list.—WILLIAM B. DAVIS, *Box 254 Faculty Exchange, College Station, Texas.*

FOR SALE—Bausch & Lomb Standard Medical Microscope, 3 objectives, incl. oil immersion; 2 oculars, Abbe substage condenser, leatherette-covered carrying case, condition excellent; $225.00, postpaid in the western U. S.—RICHARD M. STRAW, *Los Angeles State College, 855 N. Vermont Ave., Los Angeles 29, Calif.*

PRICE LIST OF PUBLICATIONS ISSUED BY THE COOPER ORNITHOLOGICAL SOCIETY

January 1, 1956

In issuing this new list we have made many changes but have endeavored to price the items as low as is consistent with our limited editions and in accordance with a recent inventory. Many of our publications are now nearly depleted and some entirely sold out. All these publications are sent post paid anywhere in the United States; for sales in California please add 3% sales tax on all items except the Condor journal.

We are continually acquiring old publications of the Society and at times can supply complete files. Send us your want list.

THE CONDOR

Vol. I (1889) "Bulletin of the Cooper Ornithological Club" - - - - - - - - - - - - *(Out of print)*

Vols. II to VII (1900-1905) The Condor *(Out of print)*

Vols. VIII to IX (1906-1907) The Condor, complete, each volume - - - - - - - - - - $12.00

Vols. X to 49 (1908-1947) The Condor, complete, each volume - - - - - - - - - - $8.00

Vols. 50 to 57 (1948-1955) The Condor, original issues complete, each volume - - - - - - $6.00

PACIFIC COAST AVIFAUNA

No. 1, 1900 Birds of the Kotzebue Sound Region, Alaska; 80 pp., 1 map - - - - - - - - - - - - $1.00
By J. Grinnell

No. 2, 1901 Land Birds of Santa Cruz County, California; 22 pp. - - - - - - - - - *(Out of print)*
By R. C. McGregor

No. 3, 1902 Check-list of California Birds; 100 pp., 2 maps - - - - - - - - - - - - *(Out of print)*
By J. Grinnell

No. 4, 1904 Birds of the Huachuca Mountains, Arizona; 75 pp. - - - - - - - - - - - - *(Out of print)*
By H. S. Swarth

No. 5, 1909 A Bibliography of California Ornithology; 166 pp. - - - - - - - - - - - - *(Out of print)*
By J. Grinnell

No. 6, 1909 Index to the Bulletin of the Cooper Ornithological Club, vol. I (1899), and its continuation, The Condor, vols. II to X (1900-1908); 48 pp. *(Out of print)*
By Henry B. Kaeding

No. 7, 1912 Birds of the Pacific Slope of Southern California; 122 pp. - - - - - - - - - *(Out of print)*
By G. Willett

No. 8, 1912 A Systematic List of the Birds of California; 23 pp. - - - - - - - - - - - - - - $ .50
By J. Grinnell

No. 9, 1913 The Birds of the Fresno District; 114 pp. - - - - - - - - - - - - - - - - $1.00
By J. G. Tyler

No. 10, 1914 Distributional List of the Birds of Arizona; 133 pp., 1 map - - - - - - - - - - - - - $2.00
(With all orders for No. 10, we include the supplement.)
By H. S. Swarth

Supplement to No. 10 by Anders H. Anderson. Reprint from The Condor, 36, 1934, pp. 78-83 - - - $ .30

No. 11, 1915 A Distributional List of the Birds of California; 217 pp., 3 maps - - - - - - - - - $1.00
By J. Grinnell

No. 12, 1916 Birds of the Southern California Coastal Islands; 127 pp., 1 map - - - - - - - - - $ .50
By A. B. Howell

No. 13, 1919 Second Ten Year Index to The Condor, volumes XI-XX (1909-1918); 92 pp. - - - - $3.00
By J. R. Pemberton

No. 14, 1921 The Birds of Montana; 194 pp., 35 illustrations - - - - - - - - - - - - - - - $3.00
By Aretas A. Saunders

No. 15, 1923 Birds Recorded from the Santa Rita Mountains in Southern Arizona; 60 pp., 4 illustrations. $ .50
By Florence Merriam Bailey

No. 16, 1924 Bibliography of California Ornithology; 2nd Installment; 191 pp. - - - - - - - - - - $2.00
By J. Grinnell

No. 17, 1925 A Distributional List of the Birds of British Columbia; 158 pp., colored frontispiece and map, 26 line maps, 12 ills. - - - - - - - - - - - $2.00
By Allan Brooks and Harry S. Swarth

No. 18, 1927 Directory to the Bird-life of the San Francisco Bay Region; 160 pp., one map, colored frontispiece - - - - - - - - - - - - - - - - - $1.00
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No. 19, 1929 Birds of the Portland Area, Oregon; 54 pp., 21 illustrations - - - - - - - - - - - - $1.00
By Stanley G. Jewett and Ira N. Gabrielson

No. 20, 1931 Third Ten Year Index to The Condor, volumes XXI-XXX (1919-1928); 152 pp. - - - $3.00
By G. Willett

No. 21, 1933 Revised List of the Birds of Southwestern California; 204 pp. - - - - - - - - - - $2.00
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No. 22, 1934 Birds of Nunivak Island, Alaska; 64 pp. - - - - - - - - - - - - - - - - $1.00
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No. 25, 1937 The Natural History of Magpies; 234 pp., colored frontispiece. Bound in paper covers - $3.00
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By Joseph Grinnell

No. 27, 1944 The Distribution of the Birds of California; 608 pp., 57 distributional maps, colored frontispiece.
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